ANNALS
OF
The Entomological Society of America

Volume XIV JUNE, 1921 Number 2

THE SCLERITES OF THE HEAD, AND THE MOUTH-PARTS OF CERTAIN IMMATURE AND ADULT INSECTS.

By G. C. Crampton, Ph. D.
(Massachusetts Agricultural College, Amherst, Mass.)

The external structures of the head, and the mouthparts in particular, are of considerable interest in making a study of the interrelationships and lines of descent of the different orders of insects; and it is of the greatest importance, in such a study, that we should know the correct homologies of the various parts, in order to determine what paths of development have been followed in deriving the higher types of insects from the lower ones. Many investigators have made the mistake of attempting to compare the higher types directly with the lowest ones without tracing the development of these types through a series of intermediate forms, with the result that the interpretations generally accepted as correct are frequently quite the reverse, and the true meaning of the different structures has not been fully grasped in many instances. On this account, I would devote the greater part of the following discussion to the consideration of such intermediate types as the Coleoptera, Neuroptera, etc., which serve to connect the lower insects with the higher ones, since it is these intermediate forms alone which can furnish us with the key to the proper interpretation of the modifications of the parts met with in the higher forms. Consideration has also been given to the condition found in larval insects as well, for, although larval insects are usually modified in adaptation to their own peculiar environmental conditions, they frequently retain the head structures in a more primitive condition than their

corresponding adults do, and the clues obtained from an examination of the larval structures have amply justified the time spent in their study.

Dr. F. C. Craighead has very generously permitted me to incorporate his observations on the musculature of the mouthparts of an adult and larval *Corydalis* in this paper, and Figures 11 and 14 of Plate III were drawn by him. Since the advance information which he has kindly permitted me to use, has not yet been published by him, I would emphasize the fact that the statements concerning the musculature of the mouthparts quoted in this paper should be accredited to him, as is indicated where such quotations have been made in the following discussion.

Through the kindness of Mr. Nathan Banks, I was able to examine a number of interesting insects in the Harvard Museum, and many of the drawings of the heads of Neuroptera were made from this material. Since the specimens were dried, however, it was not always possible to see all of the parts very clearly, and many of the drawings from this source are therefore rather diagrammatic. I am also indebted to Dr. Edna Mosher for the loan of a *Hepialis* larva, to Dr. Cornelius Betten for the identification of the trichopterous larvæ here figured, and to Dr. Needham and Dr. Tillyard for some extremely interesting and valuable neuropterous larvæ.

The principal papers dealing with the mouthparts and head structures of insects in general are those of Packard, 1882-1898; Chatin, 1884-1897; Waterhouse, 1895; Kellogg, 1902-1904; Comstock and Kochi, 1902; Verhoeff, 1904; Berlese, 1909; Crampton, 1916-1917, and Yuasa, 1920. Hosford, 1918, has also treated of the head structures of insects in general; but her paper is practically a review of Comstock's work. Peterson, 1916, has recently written a fine paper on the head structures of Diptera, comparing them with the head structures of Orthoptera; but unfortunately he did not make a study of intermediate forms connecting such primitive types as the Orthoptera with such highly specialized types as the Diptera, with the result that certain of his interpretations of the parts in Diptera are quite wrong, and other investigators such as Wesche, who have attempted to compare the structures of Diptera directly with those of Orthoptera, have fallen into the same error.

Despite the fact that a large number of papers have been published dealing with the head structures of insects, the boundaries of the various head sclerites have not in many instances been clearly defined; and in the higher insects, such as the Diptera, the parts of the labium, for example, have not been interpreted correctly in the recent papers dealing with the subject. Even the most basic and fundamental features of the composition of an insect's head are not understood and interpreted aright in most of the recent textbooks and articles which treat of this phase of the subject, and it is quite apparent that there is a decided need of a thorough-going review of the whole subject of the head region of insects and the interpretation of its parts. Thus, for example, everyone who has recently discussed the superlinguæ or "paraglossæ" of insects (i. e., the lobes on either side of the hypopharynx) homologizes them with the maxillulæ (first maxillæ), instead of with the *paragnaths* of Crustacea, as should be done. (See references to origin of superlinguæ, mandibles, maxillæ, etc., in bibliography). In most textbooks one sees the incorrect statement that the maxillary galea and palpus represent the two forks of a biramous limb, instead of the correct interpretation of the palpus as the distal segments of a limb (endopodite) in which the second or stipes segment, and the third or palpifer segment have developed endites or lobe-like processes forming the galea and lacinia. The statement that the parts of the maxillæ are represented in the mandible, which one encounters in many publications, is wholly incorrect, since the mandible represents but a single segment of a limb, while the maxilla is composed of more than one segment of such a limb. The statement that the head of an insect is composed of seven segments, instead of but six (as embryology has long shown to be the case) is another instance of the many glaring inaccuracies one encounters on every hand in reading the literature dealing with the head region of insects; but since these matters have been discussed more at length in a series of articles dealing with each phase of the subject in detail, the following discussion is restricted to an attempt to determine the boundaries of the sclerites of the head in insects in general, and to interpret the structure of the parts of the head of higher insects in terms of those of the lower forms by using for study, as far as possible, the intermediate types serving to connect the higher with the lower insects.

As the study of embryology indicates, six segments enter into the composition of an insect's head. These are the protocephalon, antennal segment, intercalary segment, mandibular segment, first maxillary segment, and second maxillary or labial segment. Janet, 1899, Berlese, 1909, and others who profess to be able to mark off the head capsule of adult insects into rings of sclerites corresponding to the embryonic segments entering into the composition of the head, have simply let their imagination run away with them, and the diagrams which they have constructed do not correspond to the facts at all, for, as embryologists such as Riley, 1904, have pointed out, "the definitive sclerites can afford us little or no evidence as to the primary segmentation of the insects." It is therefore preferable to describe the sclerites of the head with reference to certain "landmarks" which occur in most insects, rather than to attempt to divide the head capsule into rings corresponding to the original segments entering into its composition. It must be borne in mind, however, that these convenient "landmarks" for establishing the boundaries of the head regions are not present in all insects; and in some forms, the sutures, etc., which occur in the lower insects may become obliterated and new ones may be formed, thereby tending to mask the original condition, and making it very difficult to define the regions with any great accuracy throughout the series of insects. In such cases it is often impossible to do more than state that the secondarily formed region is equivalent to the original one only in a general way.

The upper lip or *labrum*, (labeled "1" in all Figures) together with the clypeus, frons, "vertex," and genæ, all arise from the first or protocerebral segment of the embryo, according to Riley, 1904; and the labrum has been compared to the prostomium of annelids by some investigators, although there is some doubt as to the exactness of the homology in the latter case. The anterior (or lower) margin of the labrum is so deeply incised in some insects, as to give the labrum a pronounced bilobed appearance, which has led certain entomologists to conclude that the labrum is the fusion produce of two appendages; but a study of the embryological development of the labrum has shown that this view is entirely fanciful and unfounded. The labrum extends posteriorly to the transverse *labral suture* which usually demarks the labrum from the clypeal region behind it, although the labral suture is obsolete in some insects. When the labrum and clypeus are viewed from the "inner" or buccal surface, a small hinge-like thickening called the *torma* by Peterson, 1916, may be observed near either end of the labral suture, at the junction of the labral and clypeal regions; and these tormæ are frequently of value in determining the posterior boundaries of the labrum.

The labrum may be long and narrow as in certain Diptera, etc., or it may be broader than long, as in the orthopteroid insects. In some Hymenoptera, the labrum is not distinct, and a membranous lobe-like region called the *epipharynx* may project from the anterior region of the mouth to close the base of the tube for sucking honey, etc. In

certain Diptera, the epipharynx may become long and stylet-like, forming with the labrum, the so-called labrum-epipharynx. In the orthopteroid insects the epipharyngeal region usually does not project to any great extent, and in such cases consists of the membranous inner lining of the labrum and clypeus (i. e., the "roof of the mouth") bearing hairs and taste organs frequently arranged about a Y-shaped thickening near the median region. In certain of these orthopteroid insects, the labrum may be partially divided into an anterior and posterior area called the *antelabrum* and *postlabrum*, by an incomplete transverse suture or by emarginations of the sides of the labrum.

As was previously mentioned, Riley, 1904, considers that the clypeus, together with the labrum, frons, etc., arose from the first or protocerebral segment of the embryo. The *clypeus*, labeled "cl" in all Figures, extends from the labrum (or the labral suture) posteriorly to the *clypeal suture*, which, however, may be obsolete in some insects. When the clypeal suture has disappeared, the posterior limits of the clypeus are demarked by a line drawn across from the base of one mandible to the base of the other mandible, since the clypeal suture, when present, corresponds in general to such a line connecting the bases of the mandibles, which are therefore the chief "landmarks" delimiting the posterior extent of the clypeus. This fact is of considerable importance, since the area usually called the clypeus in the Psocidæ, etc., lies behind the line connecting the bases of the mandibles, and is therefore in all probability an anterior portion of the frontal region.

The entire clypeal region may be but slightly chitinized and pigmented, giving the appearance of a membranous area, as is the case with the region labeled "cl" in Fig. 79 of a larval Lepidopteron, or in Fig. 39, of the termite *Mastotermes*. In other instances, as is the case in the Neuropteron *Raphidia*, shown in Fig. 33, and less clearly in the earwig shown in Fig. 36, the posterior region "pc" of the clypeus may be strongly chitinized and pigmented, while the anterior region "ac" is not strongly chitinized and pigmented (i. e., has a membranous appearance) thus differentiating the entire clypeal region into an *anteclypeus* "ac" and a *postclypeus*, "pc." Occasionally, the clypeus is divided into an anteclypeus and a postclypeus by a transclypeal suture extending transversely across it.

In the larva of the Neuropteron *Sialis*, shown in Fig. 40, the clypeal region "cl" is retained in a condition more nearly approximating the primitive, or original one. If one will compare this larva with those of the Neuroptera *Raphidia* and *Corydalis*, shown in Figs. 41 and 42, one may see that while the clypeal suture extends clear across from the base of one mandible to the base of the other in the larval *Sialis* shown in Fig. 40, (i. e., the line of the posterior border of the area "cl" extending from the base of one antenna to the other) this same clypeal suture is broken or interrupted in the larvæ shown in Figs. 41 and 42. In other words, the clypeal suture, usually extending from the base of one mandible to the other, extends only from the base of the antenna labeled "bat" to the frontal pit "fp" on either side of the head of the larvæ depicted in Figs. 41 and 42, while the median portion of the

clypeal suture has "faded out," leaving no line of demarcation between the regions "pc" and "fr." Anterior prolongations of the arms of the frontal suture "fs" have extended forward into the clypeal region and have marked off a *paraclypeal* or *lateroclypeal* region "pcl" on either side of the median region of the postclypeus "pc." Comstock and Kochi, 1902, call the paraclypeal regions "pcl" the "antecoxal pieces of the mandibles;" but they are no more closely associated with the mandibles than are the lateral regions of the clypeus in any other insects, and the *clypanguli* or postero-lateral angles or lobes of the clypeus, which frequently bear the articulatory areas with which the dorsal condyles (epicondyles) of the mandibles articulate, are very much the same in *Raphidia* (Fig. 41), as they are in any other insect. The antero-ventral arms of the tentorium frequently extend forward to a point at or near the clypanguli. In the water bug *Belostoma* (Fig. 76) the lateral areas labeled "pcl?" which are here referred to as the jugum, (following a suggestion by Dr. Parshley) are possibly homologous with the paraclypeal areas of the Neuropterous larvæ shown in Figs. 41 and 42, "pcl;" but this point has not been definitely established.

Like the labrum and clypeus, the frons is a median unpaired region of the head (the posteriormost of the dorsal unpaired areas), and it also, according to Riley, 1904, arose from the protocerebral segment of the embryo. The frons, labeled "fr" in all Figures, extends from the clypeal suture (or a line drawn between the bases of the mandibles) to the *frontal suture*, labeled "fs" in Figs. 32, 36, etc., the frontal suture, when present, serving to demark the frontal region. When the frontal suture is absent, if a line be drawn across from the top of one antennal fossa to the other, and at either end of this line an angle of forty-five degrees is constructed the sides of the isosceles triangle thus formed, correspond in a general way to the frontal suture, which is formed by the arms of the Y-shaped epicranial suture (i. e., "cs" and "fs" of Figs. 32, 36, 40, etc.) when the latter is present. The frons usually includes the area bearing the *median ocellus*, but this is absent in many insects.

The frontal suture "fs" may extend forward "inside" of (or mesal to) the bases of the antennæ, as in Fig. 32 (a condition typical of many larval insects); or it may extend "outside" of (lateral to) the bases of the antennæ, as in the earwig shown in Fig. 36. In most larvæ (Figs. 32, 40, 79) the frontal suture extends to the epicondyle, or dorsal condyle of the mandible, and this is also true of many of the adult Neuroptera here figured, although in the latter insects, only the anterior portions of the frontal suture are retained, for the most part. A pair of *frontal pits* ("fp" of Figs. 63, 70, 42, etc.) or external manifestations of the internal invaginations of the body-wall forming the antero-dorsal arms of the tentorium, occur on or near the frontal suture in many Neuroptera, etc.

As was mentioned before, the frontal suture may secondarily send down branches into the clypeal region (marking off the lateral areas labeled "pcl" in Figs 41 and 42), while the median portion of the postclypeal region "pc" unites with the frons "fr" to form a compound

frontoclypeal region bearing the labels "fr" and "pc" in Figs. 41 and 42, although the original extent of the frons "fr" is retained in the insect shown in Fig. 40.

A line drawn across between the bases of the antennæ divides the frons into an *antefrons* and *postfrons* in certain insects, and in these forms, the postfrons is usually united with the upper region of the head capsule. A narrow transverse region called the *epistoma* "eps" of Fig. 38, becomes secondarily marked off in the anterior region of the frons of certain beetle larvæ, etc., and in certain sawfly larvæ, such as the one shown in Fig. 32, a region labeled "eps," which may correspond to a portion of the epistoma is marked off by a faintly impressed line. MacGillivray, 1913, refers to the region "eps" of the sawfly larva shown in Fig. 32, as the "first clypeus," and to the true clypeus "pc" and "ac" as the "second clypeus." The region "eps," however, is clearly a portion of the frons, since it lies behind the clypeal suture extending across from the base of one mandible to the other, and while the region labeled "eps" in Fig. 32 does not correspond to the entire area bearing the label "eps" in Fig. 38, it does in a way correspond to the epistoma, or to a portion of the epistoma, and may therefore be regarded as a greatly reduced epistoma.

It is possible that the area labeled "fr" in Fig. 76 represents the anterior region of the frons (antefrons) rather than the frons proper, although for the sake of convenience, it has been referred to simply as the "frons" in the following discussion. In the Psocidæ (sensu lato), however, the region usually referred to as the "frons" is clearly the antefrons (or anterior region of the frons) alone, while the posterior region of the frons in these insects is frequently indistinguishably united with the region of the head behind it.

The frons was spoken of above as an unpaired region of the head, and this is true of most insects. In the beetle larva shown in Fig. 38, however, a median dorsal infolding or "implex" of the head capsule is formed, resulting in the production of an internal ridge for muscle attachment, and an external suture (corresponding to the internal ridge) which extends forward into the frontal region "fr," dividing it into equal halves,* as is shown in Fig. 38.

If we adopt from vertebrate anatomy the term "frontal region" for the frons, and the term "occipital region" for the portion of the head capsule about the occipital foramen, it is but logical to call the region between the frontal and occipital regions the "parietal region," since the parietal region occupies this position in the vertebrate skull. The term "parietals" has therefore been adopted for the region between the frons and occiput (i. e., the region labeled "pa" in all Figures) in the following discussion. Some entomologists apply the term epicranium to the parietals; but properly speaking, the epicranium includes not only the parietals, but also the frons, genæ and postgenæ as well, and it is preferable to have a distinct designation for the parietals.

*It is quite probable that the region labeled "fr" in Fig. 38 represents the post frons, rather than the entire frons, since it lies behind the antennæ (in the postfrontal region).

The term vertex has also been applied to the parietals, and while this term is quite suitable for the parietal region of the Orthopteroid insects, in which the parietal region occupies the upper portion of the head, in other insects, such as the lepidopterous larva shown in Fig. 79, in which the parietals extend far forward, the term vertex is wholly inapplicable for the region in question, and in order to have a suitable term for this region in all insects, and since the sclerites composing this region are *paired*, it is preferable to refer to the sclerites between the frons and occiput as the parietals, as is done in vertebrate morphology.

The stem of the Y-shaped *epicranial suture* "cs" and "fs" forms the *midcranial* or *coronal suture* "cs" dividing the parietal area into symmetrical parts, and it is usually along this suture that the integument of the insect splits at the time of molting. The coronal suture "cs" is likewise an anterior continuation of the middorsal suture along the median region of the back, along which the integument of the body in general is split at the time of molting, thus suggesting a Lamarkian explanation of the origin of the suture in question. Comstock and Kochi, 1902, state that the middorsal suture "represents the line of closure of the embryo." While this suture may coincide with the line of closure of the embryo, I am inclined to consider that the middorsal suture (and its continuation into the head region as the coronal suture "cs") in some cases owes its origin to an infolding of the integument for muscle attachment. In the head region there is frequently a median dorsal "implex" or endoplica formed by an infolding of the integument for muscle attachment, and the lips of such an infolding of the body wall form an external suture.

In certain lepidopterous larvæ, as in the one shown in Fig. 79, an infolding of the integument occurs on either side of the frontal region "fr," and the *frontal sutures*, formed by the lips of these infoldings or endoplicæ, together with the *adfrontal sutures* mark off an adfrontal area (the *adfrontals* "af") on either side of the frons. In the beetle larva shown in Fig. 38, there are also marked off on either side of the region labeled "fr" (which represents a posterior portion of the frons) areas resembling the adfrontals "af" of the Lepidoptera (Fig. 79); the sclerites labeled "af" in Figs 38 and 79, and although the regions are not precisely the same in both insects, may be referred to as the adfrontals, for the sake of convenience.

On either side of the frons "fr" of various Neuroptera (e. g., Figs. 45, 56, 70, 74, etc.) there occurs a *parafrontal region* or *parafrons*, "pf," usually situated between the frontal suture (or the frontal pits "fp") and the compound eyes. The parafrontals are therefore somewhat different from the adfrontals described above, and have been designated by another term, to indicate this fact.

As was pointed out in a paper on the head region of lower insects (Crampton, 1917) a "*paracephalic*" or *laterocephal* suture marks off a laterocephalic area on each side of the head capsule, in some of the lower forms, though these areas may possibly represent secondarily

formed regions of no particular phylogenetic significance, since they are not demarked in all of the primitive insects.

The anterior portions of the laterocephalic regions, namely, the areas below and behind the compound eyes, forming the "cheek" regions of the head, are called the *genæ*. An approximately vertical ridge or suture frequently demarks a posterior region of the genæ called the *postgena* by Comstock and Kochi, 1902. When these postgenæ extend along the gular region of the head, they correspond in a way, to the paragular region and hypostoma, described under the discussion of the ventral surface of the head capsule.

At the base of the mandibles (below, or anterior to the genæ) is a small sclerite called the *basimandibula* ("bmd" of Fig. 39) in the article referred to above (Crampton, 1917). This sclerite probably owes its origin to the chitinization of a portion of the membrane between the mandible and the head capsule. Comstock and Kochi, 1902, call the sclerites "bmd" (Fig. 39) the "trochantin of the mandible," thinking that it represents the trochantin or small sclerite at the base of the thoracic legs. This homology, however, is entirely fanciful, and it is misleading to designate the sclerite in question as the "trochantin" of the mandible.

Comstock and Kochi, 1902, describe an *occular sclerite* surrounding the compound eyes; but I am inclined to consider that this area is not marked off by a true suture, and I am very sure that it does not represent the basal segment of an occular appendage as Comstock and Kochi, 1902, are inclined to believe. There is, however, in certain lower insects, a fairly well demarked sclerite at the base of the antenna, called the *antennale* in a previous paper (Crampton, 1917); and a process or projection of this region called the *antennifer* in the paper in question (i. e., the structure labeled "anf" in Fig. 39), frequently supports the antenna in the more primitive insects. At the base of the antenna of many larval insects (particularly those of Coleoptera and Neuroptera) a ring-like area called the *basantenna* ("bat" of Figs. 41, 42, etc.) occurs at the base of the antenna. This area may originate as a projection of the head capsule, or through the chitinization of a portion of the membrane at the base of the antenna, and I am inclined to account for its origin in either of these ways, although this sclerite is regarded as a modified basal segment of the antenna by some entomologists.

Areas called the *postcranial regions*, or the *postcranials* (Crampton, 1920) occur in the posterior portion of the head of certain Trichoptera, etc. Traces of these regions are also found in the lower Lepidoptera, such as the Micropterygids, etc., but I have not traced them through a series of the more primitive representatives of the higher insects, though they will doubtless be found in other orders as well.

The *occiput* labeled "ocp" in all Figures is the dorsal and lateral region about the *occipital foramen*, or posterior opening of the head capsule through which the gullet, nerve cord, etc., pass into the head region. A posterior extension of the midcranial suture "cs" divides the occiput into two parts in the larva of the Neuropteron *Corydalis* (Fig. 42), and in the beetle larva shown in Fig. 38, the occiput consists

of two *occipitals* "ocp" separated by a deep incision. The membranous area occupying the region between a similar incision in the posterior region of the head of the caterpillar shown in Fig. 79, and the anterior edge of the pronotum, is called the *vertical triangle* by Fracker, 1915.

In the postero-lateral region of the head, there frequently occurs a narrow area called the *trophifer* (Crampton, 1917) since the mouthparts articulate with this region in the lower insects. The *maxillifer* (or "*maxillary pleurite*" of Comstock and Kochi, 1902) enters into the composition of this region, and Riley, 1904, states that a portion of the postgena together with the "maxillary pleurite" arises from the maxillary segment, while the remainder of the postgena and the sclerites at the base of the mandibles arise from the mandibular segment of the head. It is very strange that if the basimandibulæ "bmd" of Fig. 39 belong to the mandibular segment, the genæ immediately above them do not belong to this same mandibular segment (Riley attributes the genæ to the protocerebral or first primitive segment of the head) and I am not entirely convinced of the correctness of Riley's conclusions in this matter, especially since he wrongly ascribes the cervical sclerites to the labial segment. Riley does not state to which embryonic segment the occiput belongs; but since the occiput occupies a considerable portion of the hinder region of the head, it is quite probable that it is derived from both the maxillary and labial segments.

According to Comstock and Kochi, 1902, the occiput is continued ventrally in the postgenæ, but in certain insects having a well defined occipital region (as in the neuropterous larvæ shown in Figs 14 and 15) the occiput extends ventrally to the gular region "gu." In the beetle shown in Fig. 17, it would appear that the occiput "ocp" is secondarily marked off by the rubbing of the prothoracic parts into which the hinder portion of the head is received in these insects.

The mandible articulates ventrally (by means of the hypocondyle, or ventral condyle labeled "hc" in Fig. 14, etc.) with a region called the *hypostoma*,* labeled "hs" in all Figures. The hypostoma "hs" is an antero-ventral region of the head (a portion of the region called *postgena* by Comstock and Kochi, 1902) situated on either side of, or near, the submentum "sm" (Figs. 15, 17, 18, 9, etc.), and is frequently demarked by a *hypostomal ridge* (or *suture*). Its chief distinguishing feature, however, is the fact that it bears the area with which the ventral condyle of the mandible articulates. In many insects it also bears a "fossa" in which the condyle of the maxilla articulates.

The *paragula* is a region on either side of the gula, labeled "pgu" in all Figures, and is demarked laterally by the paragular ridge or suture. The paragular area is indicated by the shaded area "pgu" (in Figs. 31, 13, 6, 7, 10, etc.) and forms the postero-ventral region of the head on either side of the gula "gu." The paragula and hypostoma together

* This region in larval Cleridæ is discussed by Boving and Champlain in the Proceedings of the U. S. Nat. Museum, Vol. 57, p. 575, 1920, in which a discussion of the mouthparts of Coleoptera in general are also given. The term paragula is also employed in this paper.

make up the region called the postgena by Comstock and Kochi, 1902, the hypostoma forming the anterior portion near the mouth, while the paragula forms the posterior portion of the postgena. It has seemed advisable to thus divide the postgena, since the hypostoma in particular is of importance in the study of the head structures of larval Coleoptera, Neuroptera, etc. In the beetle larva shown in Fig. 27, a small sclerite "pgu?" situated on either side of the gula "gu," and bounded posteriorly by a paragular suture, has been provisionally homologized with the paragula of other insects, although it very probably represents merely an anterior portion of the entire paragula. The divided areas labeled "pgu" in Figs. 22 and 29 are likewise not strictly homologous with the paragulæ of other insects, but it is not worth while to designate them by a distinct designation, since they occupy approximately the position of the paragular areas.

The throat region, or the median postero-ventral area of the head, labeled "gu" in all Figures, is called the *gula*. The gula "gu" extends from the posterior border of the head capsule proper to the submentum "sm" (Figs. 12, 16, 15, 18, etc.) and is bounded laterally by more or less distinct lines or sutures called the *gular sutures*. Situated on or near these sutures are the *gular pits* "gp" of Figs. 15, 12, 9, etc., which mark the position of the posterior ventral arms of the tentorium. In some insects, the gular pits mark the posterior extent of the submentum, but in others, the gular region extends far forward of these gular pits (as in Fig. 12). In such cases, the anterior extent of the gular region is marked by a line drawn between the bases of the maxillary cardines "car" (corresponding to the submental suture), or, according to Dr. Craighead, the gular region extends forward to the posterior attachment of the muscles labeled "11" in Figs 11 and 14.

The *intersternite*, "is" of Figs 8, 15, 13, etc., one of the anterior plates of the neck region, is ascribed to the gular region by Comstock and Kochi, 1902, Riley, 1904, and others; but this plate becomes attached to the posterior region of the head in very few insects, and then only secondarily. It is homologous with other intersegmental plates occurring between the thoracic segments in the lower insects, as was pointed out by Crampton, 1917. The *pregula*, "prg" of Fig. 17, is apparently a region secondarily marked off in front of the narrow region of the throat labeled "gu" in certain Coleoptera, etc. Its significance is not very clear, and there is need of further study of this region.

In the insects shown in Figs. 20, 21, 24, 26 and 27, the region labeled "gu" may not represent the entire gula, and has therefore been referred to as the *gular plate* in the following discussion. The region labeled "gu" in Fig. 7, likewise may not represent the entire gular region, but such a narrow, transverse, posterior gular plate is characteristic of the Dermaptera, and may serve as one of the diagnostic characters of the order.

The origin of the gular region is a very puzzling feature. It is quite possible that in some insects the posterior portion of the gular region of the adult head may be formed through a chitinization of the membranous area situated between the ventro-median edges of the head

capsule and behind the mentum. In the insect shown in Fig. 27, it would appear that the ventro-median edges of the head capsule have become approximated, or "come together," behind the narrow gular plate "gu," and meet along the ***midgular suture*** "mgs." The fact that there is a narrow membranous space behind the gular plate "gu" in the trichopterous larva shown in Fig. 20, while this space has apparently disappeared through the coming together of the median edges of the head capsule behind the gular plate "gu" in the trichopterous larva shown in Fig. 24 (in which there is a midgular suture "mgs" like that of the beetle larva shown in Fig. 27) would lend weight to the view that the midgular suture "mgs" is formed by the approximation of the ventro-median edges of the head capsule along the median line of the head. On the other hand, the midgular suture "mgs" of Figs. 24 and 27, may have been formed secondarily in the integument of the head capsule as the result of the formation of a midventral implex or infolding of the body wall, such as frequently occurs along the midventral line of the thoracic region. Comstock and Kochi, 1902, suggest that the midventral suture of the thoracic segments "perhaps represents the neural groove of the embryo;" but I am inclined to attribute another origin to the suture in question—which probably arose through the formation of an infolding of the body wall for muscle attachment.

A study of the condition found in the different castes of termites throws some light upon the rather difficult question of the origin of the gular region, since in the termites, at least, the gular region appears to represent the posterior portion of an originally distinct plate which has become adherent to the head capsule. Thus, for example, in the head of a winged termite such as that shown in Fig. 13, the gular region "gu" forms the posterior portion of a distinct ***gulamental plate*** bearing the labels "gu" and "sm." In the soldier caste of this same termite, on the other hand, the posterior portion of the gulamental sclerite (bearing the labels "sm" and "gu" in Fig. 16) becomes "soldered onto" the head capsule to form the gular region, "gu," while the anterior portion of the gulamental area, bearing the label "sm," remains free and forms the submental region. We may therefore conclude that in some cases at least, the gulamental plate ("gu" and "sm" of Fig. 13) becomes elongate and its posterior portion is more or less closely fused with the head capsule to form the gular region "gu" of Fig. 16. In such instances, the lateral margins of the plate in question may be represented by the ***gular sutures*** on either side of the gular region "gu" shown in Fig. 16.

The ***labium*** or under lip is formed by the union of a pair of mouthpart-limbs (second maxillæ) similar to the maxillary mouthparts. The statement so often made that the neck plates, or cervical sclerites, represent the labial segment whose appendages have left the neck region and have migrated into the head region to form the labium, is wholly false, and is unsupported by a single bit of anatomical or embryological evidence. This matter, however, has been fully discussed in an article by Crampton, 1917, and need not be further considered here.

The pleural region of the labial segment is included in the region about the occipital foramen referred to as the "trophiger" or trophi-bearing area, and forms the narrow marginal area shown in Figs. 13, 10, etc. It sometimes bears an *occipital condyle* or process, with which the anterior process of the lateral neck plate articulates to aid in supporting the head capsule, while allowing for the freedom of movement of the head.

Holmgren, 1909, states that "an embryological study (of the second maxillæ or labial appendages) further indicates that the submentum is formed by a portion of the articulatory membrane between the second maxillary segment (or labial segment) and the first thoracic segment, and therefore has nothing to do with the second maxillæ (labial appendages)." Holmgren, Heymons, and other embryologists likewise agree that the hypopharynx or "tongue" is formed in part by the sternum of the labial segment, and Boerner, 1903, states that he considers it quite impossible to regard the mentum, submentum and gula as the sternites of the labial segment, "since in some insects, traces of a true (labial) sternum are retained between the bases of the coxæ of the posterior mouthpart-limbs." In other words, Boerner regards the median triangular area between the bases of the structures labeled "pgr" in Fig. 10, as the representative of the sternum of the labial segment. Whether these views are correct or not, I cannot say, although I have a strong feeling that either the mentum, or a portion of the submentum may be formed from the sternal area of the labial segment (in addition to the basal portion of the hypopharynx which is formed from the sternal area of the labial segment). What proof there is to be drawn from embryology, however, would not bear out the latter view—at least so far as is at present known; and under these conditions, it would be wholly unjustifiable to claim that the mentum, or a part of the submentum are formed from a portion of the sternal region of the labial segment. On this account, I have provisionally accepted the view that the submentum and mentum are secondarily formed sclerites situated behind the true labium, in the following discussion. It has been found convenient, however, to treat the underlip as though it were composed of three principal plates or areas, in comparing this region in the different types of insects; and for the sake of convenience, I have referred to these three plates or areas as the ***gulamentum*** (i. e., the region bearing the labels "gu" and "sm" in Fig. 23), the ***mentum***, labeled "mn" in Fig. 23, and the true labium, or ***eulabium***, which bears the labels "prm," "lg" and "lp," in Fig. 23.

The ***gulamentum*** ("gu" and "sm" of Figs. 23, 13, etc.) becomes divided into a gular region and a submental region in some insects, while the gular portion becomes "soldered" onto the head capsule in some insects (e. g., "gu" of Fig. 16) as was stated above; and the gular region may be further augmented by the addition of portions of the integument behind the gulamentum. The gular region "gu" is separated from the ***submentum*** "sm" by a ***pregular cleft***, or ***suture***, in such insects as the caddice fly larva shown in Fig. 24, and the occurrence of such a pregular suture is of value in marking off the posterior extent of

the submentum. The suture in question, however, is rarely present in insects in general, and in such cases the posterior limits of the submentum are demarked by an imaginary line drawn across from one gular pit "gp" of Fig. 15, to the other gular pit, or by a line drawn across from the base of one maxillary cardo "car" of Fig. 12, to the other, and corresponding in general to the line behind the label "sm" in Fig. 12. Dr. Craighead informs me that the submento-mental muscles labeled "11" in Figs. 11 and 14, which extend from the posterior border of the submental region to the posterior portion of the mental region, serve to demark the submental region "sm," internally; and since the posterior line of attachment of these muscles corresponds in a general way to the posterior border of the submentum, they offer a valuable means of determining the homologues of the submental region when it is not clearly demarked externally. The most reliable method of determining the posterior limits of the submentum on the external surface of the head, however, is to draw an imaginary line between the bases of the cardines "car" of Figs. 24, 21, 20, 26, 31, 22, 9, 8, 7, etc., since it is not always possible to dissect a specimen (e. g., as is the case with dried material) in order to determine the origin and insertion of the muscles in question.

In the insects shown in Figs. 21, 22, etc., the submental region contains two small plates, the *submentales*, "sml," situated at the base of the maxillary cardines "car." These submentals do not comprise the entire submental region, and in some insects, such as the one shown in Fig. 20, the submentals are represented by the small areas labeled "sml" alone. In the lepidopterous larva shown in Fig. 25, the areas labeled "sml" occupy a position at the bases of the maxillary cardines, "car," as do the submentals of the insects referred to above; and the areas labeled "sml" in Fig. 25, as well as the ill-defined areas bearing the label "sml" in Fig. 29, may therefore be interpreted as representing the submentals of other insects. In the caterpillar shown in Fig. 28, the submentals "sml" are rather heavily chitinized and pigmented, and might be mistaken for the maxillary cardines, but the true cardo of the maxilla is the plate labeled "car" in Fig. 28. The submental region is membranous in some insects, such as those depicted in Figs. 31, 77, etc., while in such insects as the beetle, shown in Fig. 17, "sm," it is strongly chitinized and is deeply emarginate anteriorly.

In the Neuropteron *Nemoptera* (Fig. 86) and in the Mecopteron *Bittacus* (Fig. 85) the principal part of the submentum "sm" forms a portion of the slender column-like sclerite whose anterior region "mn" has been homologized with the mentum; and this tendency toward the formation of a column-like sclerite in the mental region is also found in some Diptera. Whether the submentum includes the entire plate bearing the label "sm" in Figs. 10 and 6, or not, I cannot say; but it is very probable that the plate in question contains the gular region as well. It is also possible that the anterior, paler area bearing the label "sm" in Fig. 6, represents an anterior division of the submentum.

The *mentum*, "mn" of Figs. 5, 6, 7, 8, 9, 10, 23, 31, 12, 15, 77, etc., is the region between the submentum, "sm," and the eulabium, or true

labial region bearing the labels "pgr," "ls," "prm," etc., in the figures in question. The mentum "mn" forms the second of the plates forming a series of three in the underlip region of the Neuropteron shown in Fig. 23, which I have taken as the basis for comparison with the higher insects. The mentum, "mn," may be fused with the region "sm" behind it, as in the insects shown in Figs. 85, 86, etc.; it may be separated from the submental region "sm" by a clearly defined ***mental suture*** as in Figs. 23, 26, 7, etc.; it may be demarked merely by a faint dividing line between it and the submental region as in Fig. 13, etc.; or it may be a distinct plate "mn" as in the insects shown in Figs. 82, 77, 15, 6, etc. In the insects depicted in Figs. 21, 31, 17, etc., the mentum is represented by a membranous area bearing the label "mn." The ***mentales*** or small sclerites bearing a seta and situated in the posterior region of the mentum, "mn" of the caterpillar shown in Fig. 31, or in the trichopterous larvæ shown in Figs. 21, 20, etc., are possibly homologous with the chitinized areas in the posterior region of the mentum "mn" of the Neuropteron larva shown in Fig. 12.

The ***eulabium*** comprises the distalmost, or anteriormost portion of the underlip region beyond the mentum, "mn," from which it is separated by a ***eulabial suture*** in the insects shown in Figs. 23, 20, 27, 13, 15, 17, etc. The eulabium, as was stated above, is the true labium, formed by the union of the second maxillæ. I would emphasize the fact that the labial appendages are homologous with the second maxillæ of the Crustacea (see articles in bibliography) and it is wholly incorrect to maintain that the so-called superlinguæ on either side of the hypopharynx of insects are homologous with the first maxillæ (i. e., the maxillulæ) of Crustacea as is done by practically all recent investigators, since the "superlinguæ" are homologous with the ***paragnaths*** of Crustacea, and the labial appendages represent the true second maxillæ of Crustacea, as has been brought out in a paper published in the 50th. Annual Report of the Ent. Soc. of Ontario, in a preliminary note in the Transactions of the Ent. Soc. of London, and in a more lengthy paper on this subject, illustrated by drawings of the parts in question in Crustacea and insects, which will soon be published in Psyche, and the Proc. Ent. Soc. Washington for 1921.

As was mentioned in the preceding discussion, the greater portion of the sternum of the labial segment enters into the composition of the ***hypopharynx***, or tongue-like structure on the floor of the mouth cavity. It is very probable, however, that the ***labiosternite*** or median triangular area between the bases of the structures labeled "pgr" in Fig. 10, represents a portion of the sternal region of the labial segment. The ***palpigers***, "pgr," or palpi-bearing structures on either side of the median triangular area shown in Fig. 10 (also structures labeled "pgr" in Figs 6, 7, 15, 81, etc.) together with the labiostipes, "ls," represent portions of the basal segments of the modified limbs forming the labium, while the distal segments of these limbs (representing the terminal segments of the "endopodite" of a crustacean limb) form the ***labial palpi*** "lp" of Figs. 6, 7, 10, 15, etc. Outgrowths of the basal segments "pgr" and "ls" of the limbs (these outgrowths possibly represent endites or "gnath-

obases" of a crustacean limb) form the ***glossa***, "gl," and ***paraglossa***, "pg," of the labium (see Figs. 6, 10, etc.) The glossæ, "gl," of Fig. 13, 10, etc., are sometimes referred to as the inner lobes of the labium, while the paraglossæ "pg" are sometimes referred to as the outer lobes of the labium. The sclerite labeled "ls" in Figs. 10, 6, 13, etc., is sometimes called the "stipes," but since the term stipes is restricted to a sclerite of the maxilla, I would refer to the sclerite "ls" as the ***labiostipes***, to indicate that it is a labial structure. The labiostipes "ls" bears the inner and outer lobes of the labium (i. e., "gl" and "pg" of Figs. 6, 10, etc.) in some insects.

Various modifications of the above-mentioned structures are met with in different insects. Thus in the beetle larva shown in Fig. 8, a ***ligula***, labeled "lg" occurs in the region originally occupied by the inner and outer lobes ("gl" and "pg" of Figs 10, 6, etc.), and it is quite probable that the ligula "lg" of the beetle larva shown in Fig. 8, (or the insects depicted in Figs. 9, 49, 23, 27, etc.) represents the fusion product of the two inner lobes (glossæ) of the labium, with which the outer lobes (paraglossæ) may also have united. In the insects shown in Figs. 17 and 15, on the other hand, the ligula "lg" is apparently formed by the united glossæ only, since the paraglossæ "pg" are apparently still distinguishable. In most instances, however, the general term ligula has been applied to the unpaired median terminal structure projecting between the labial palpi (i. e., "lg" of Figs. 8, 9, 27, 23, etc.) regardless of whether it is formed by the united glossæ alone, or whether the paraglossæ have also entered into its composition.

In the larvæ shown in Figs. 8, 20, 25, 31, 49, etc., there occurs a ***basilabium***, "prm," or basal labial plate formed by the union of the labial stipes "ls" of Figs. 6, 10, etc. This basal labial plate may also include the palpigers in its composition, and is typically a transverse chitinization of the area at the base of the labial palpi. In some insects it is not demarked from the ligula "lg" (as in Figs. 23, 9, etc.) while in others, such as those depicted in Figs. 8, 22, etc., it is demarked by a faint line, or is differentiated by a stronger chitinization and pigmentation.

In connection with the discussion of the terminal region of the labium, the ***spinneret*** "spt" of Figs. 25, 31, etc., should be mentioned. This spinneret is usually closely associated with the ligular region, although a portion of the hypopharynx may possibly be involved in the spinning structure. Whether or no the structure labeled "spt?" in Fig. 30, is homologous with the spinneret of lepidopterous larvæ, is a question which I have been unable to decide, and I have therefore merely offered the suggestion as a possibility, rather than as a definite opinion in the matter. A comparative study of this region in the Trichoptera, Lepidoptera, and other spinning larvæ is greatly needed, and would be of considerable value in the matter of determining the affinities of the insects having caterpillar-like larvæ.

It is very unfortunate that Peterson, 1916, who follows Kellogg, 1899-1902, in his interpretation of the parts, did not study the mouthparts of the Neuroptera such as *Nemoptera* (Fig. 86) and the Mecoptera,

such as *Bittacus* (Fig. 85), *Panorpa* (Fig. 82), etc., before attempting to homologize the parts in the highly specialized order Diptera, instead of attempting to compare the Diptera directly with the lower orders such as the Orthoptera, etc., since the Neuroptera and Mecoptera mentioned above furnish the key to the interpretation of the parts in the Diptera, and the evidence they offer is most convincing. Wesche, however, is probably responsible more than anyone else for the confusion of the interpretation of the parts of the trophi by recent Dipterists, and Peterson's work is a great improvement over that of Wesche, Smith and others who have misinterpreted the structure of the mouthparts in a most amazing fashion, due to the fact that they have ignored the intermediate forms between the lower orders and the higher ones in attempting to homologize the parts in Diptera.

As I pointed out in a recent paper (Crampton, 1917) dealing with the head region of Neuroptera, Mecoptera, Diptera, etc., the labial palpi, "lp," of the Neuroptera such as *Nemoptera* (Fig. 86) tend to become approximated in the median line of the head (compare Fig. 86 with the Neuropteron shown in Fig. 81) while the ligula "lg" tends to disappear. A further step is represented by the Mecopteron shown in Fig. 85, in which the ligula "lg" of Fig. 86 has completely disappeared, although the labial palpi, "lp," have retained their typical three-segmented condition, and the palpigers, "pgr," are still partially distinct. In the Mecopteron shown in Fig. 82, the labial palpi, "lp," have been reduced to two segments, the basal one being quite thick and "fleshy," while the terminal one is small and slender. The sclerites which I have interpreted as the palpigers, "pgr," (although they may possibly represent the basal segments of the labial palpi instead) tend to unite, and the mentum "mn" is a broad plate somewhat produced anteriorly. A further modification is shown in the Mecopteron depicted in Fig. 84, the labial palpi being reduced to the fleshly lobes, "lp," while the palpigers have united to form the region "pgr," which is but indistinctly demarked from the mentum "mn" behind it. The labial palpi, "lp," have even developed "pseudotracheæ" like those occurring on the labial lobes of certain Diptera, in some of the Mecoptera; and the whole trend of development in the Mecoptera indicates the origin of the inherent tendencies which find opportunity for fuller expression in the Diptera. Thus in the Dipteron shown in Fig. 83, the labial palpi "lp" are fleshy lobes like those of certain Mecoptera,* and they have even retained traces of two segments in the Dipteron shown in Fig. 83, which in this respect is more primitive than the Mecopteron shown in Fig. 84. The palpigers, "pgr," of Fig. 83 are also distinct, although they have completely united in the insect shown in Fig. 84, to form the region labeled "pgr." The narrow median structure labeled "mn" in Fig. 83, is clearly the mentum. When one compares the Diptera with the

* Dr. Tillyard, to whom I have shown the accompanying figures, in discussing the interpretation of the mouthparts of the Diptera, informs me that he has come to the same conclusion, independently, in comparing the head structures of Diptera with those of the Mecoptera, thus giving additional weight to the correctness of the interpretation here offered.

Mecoptera and with the Neuropteron shown in Fig. 86, it is thus a very simple matter to determine the interpretation of the parts of the labium of the Diptera, and if Peterson and Wesche had only used these forms instead of trying to compare the Diptera directly with the Orthoptera, etc., they would have had no difficulty in determining the homologies of the Dipteron structures, so far as the principal features of the mouthparts are concerned. I must admit, however, that the interpretation of the slender lobes between the terminal segments of the labial palpi labeled "lp" in Fig. 83, has given some trouble. They may possibly represent the paraglossæ ("pg" of Fig. 77), for example) of other insects, although I am more inclined to regard them as merely lobe-like outgrowths of the segments of the palpi.

The interpretation of the parts of the labium of the hemipterous insects has proven to be a rather difficult problem, largely due to the fact that I have not as yet been able to make a thorough study of the mouthparts of the Psocidæ (which are closely related to the hemipterous insects) due to lack of proper material. From what is known of the tendencies for the parts to unite in the Mecoptera discussed above, however, I think we are justified in assuming that the sclerites labeled "lp" in Fig. 75 (of a species of *Cicada*) represent the more or less closely united labial palpi, while the structures labeled "pgr" in Fig. 75, very probably represent the palpigers "pgr" of Figs. 82, 86, 83, etc., and the plate "mn" of Fig. 75 is therefore largely composed of the mentum; the other basal structures of the underlip region are probably included in the more membranous region behind the mentum "mn." When we turn to the true Hemiptera (Heteroptera), however, the parts have become so modified that it is very difficult to determine their homologies in many instances. Dr. Parshley has called my attention to the fact that hemipterists frequently interpret the structures labeled "ap" in Fig. 76, as the "labial palpi" in the belostomatids; but Heymons does not consider that the structures in question are the true labial palpi, from his embryological studies. I am more inclined to regard the appendages "ap" of Fig. 76, as lateral lobes of the region "pgr," which have become demarked by the formation of a secondary suture; and the appendages "ap" therefore have nothing to do with the true labial palpi, which probably enter into the composition of the sclerite labeled "lp?" in Fig. 76. The structures labeled "pgr" and "mn" in Fig. 76, are possibly the palpigers and mentum, "pgr" and "mn," of the *Cicada* shown in Fig. 75.

I would call attention to the fact that in all of the coleopterous larvæ which I have examined, the labial palpi, when well developed, are made up of not more than ***two segments***, while in all of the neuropterous larvæ which might be mistaken for coleopterous larvæ have at least ***three segments*** in the labial palpi. This distinction may be of value in distinguishing between the two types of larvæ, since it is very difficult to find any characters for differentiating between the two groups of insects, and any distinguishing feature which "holds good" in the majority of cases, should be of considerable interest on this account.

The Dermapteron shown in Fig. 7 is a primitive, but highly aberrant earwig, and the condition occurring in its mouthparts may therefore not be as typical as though another form had been chosen to illustrate the group. In all of the Dermaptera which I have examined, however, the paraglossæ "pg" (Fig. 7) are long and slender, and the glossæ have apparently been lost, so that these features, in conjunction with the peculiar character of the gula "gu" (which is a narrow transverse sclerite in the earwigs) may be of value in characterizing the order Dermaptera.

In the larvæ of the Neuroptera related to the Myrmeleonidæ (Figs. 44 and 47) there is a tendency for the gula, "gu," submentum, "sm," and mentum, "mn," to unite, while the antero-lateral structures labeled "pgr" bearing the labial palpi, "lp," acquire a greater mobility to compensate for the loss of movement on the part of the rest of the labial structures. The structure labeled "pgr" in Figs 44 and 47 may not be the exact homologues of the palpigers "pgr" of other insects; since other portions of the labium probably enter into their composition; but the term palpiger as applied to the structure in question is sufficiently accurate for practical purposes. In the neuropterous larva shown in Fig. 46, the labial palpi are apparently composed of more than the usual three segments found in the palpi of most Orthoptera, etc., and it is quite probable that a secondary segmentation of the palpi has taken place in the Neuropteron in question. Faint indications of such a secondary segmentation of the labial palpi, "lp" are to be found in the larva shown in Fig. 51, in which the labial palpi are either composed of but three actual segments, with a distinct palpiger having the appearance of a fourth segment, or a fourth segment has been formed in an originally three segmented labial palpus. The fact that the palpi are but three-segmented in the primitive neuropterous larvæ shown in Figs. 23, 12, 15, etc., would indicate that three is the original number of the labial segments of the group as a whole. In connection with the discussion of the labial palpi of the Neuroptera, I would call attention to the *palpimaculæ*, "pm," or sense organs borne on labial palps of the Myrmeleonid shown in Fig. 70. A similar sense organ occurs on the labial palp of *Nymphes* (Fig. 72, "pm") and this fact adds weight to the view that the Myrmeleonidæ and Nymphes are quite closely related.

The *maxillæ* of an insect are homologous with the first maxillæ (not the second maxillæ, as Folsom and others maintain) of Crustacea, as may be seen by comparing an embryo of any primitive insect, with the embryo of a crustacean, such as the isopodan *Jaera*, figured by McMurrich. The sternal region of the maxillary segment takes part in the formation of the hypopharynx, or tongue-like structure on the floor of the pharyngeal cavity, while the pleural region of the maxillary segment enters into the composition of the posterior region of the head, called the "trophiger," which is situated near the occipital foramen, or posterior opening through which the nerve cord, gullet, etc., pass into the head capsule. The pleural region of the maxillary segment is demarked from the pleural region of the labial segment behind it by

the posterior tentorial invaginations, according to Riley, 1904, in the embryo of the cockroach.

The membrane at the base of the maxilla, labeled "bm" in Fig. 5, etc., may be termed the ***basimaxillary membrane***. A plate called the ***basimaxilla***, "bm," of Figs. 8, 9, etc., results from the chitinization and pigmentation of the membranous region at the base of the maxilla in certain coleopterous larvæ, etc. This basimaxillary plate, "bm," of Figs. 8 and 9, should not be confused with the subdivision of the cardo labeled "pac" in Figs. 5, 6, etc., since the latter sclerite, "pac," is a demarked subdivision of the cardo, and therefore does not arise through a greater deposition of chitin and pigment in the membrane at the base of the maxilla, as is the case with the basimaxillary plate.

As was pointed out in a paper dealing with the maxillæ of orthopteroid insects (Crampton, 1916) the basal sclerite or ***cardo*** of the maxilla of the insect shown in Fig. 10, for example, is divided into a ***eucardo***, "euc," and a ***paracardo***, "pac," while the ***stipes***, or second segment of the maxilla, is divided into a ***eustipes***, "eus," and a ***parastipes***, "pas." The parastipes, "pas," however, is apparently a distinct narrow sclerite formed along the mesal margin of the stipes, and it is doubtful that it arose as a demarked portion of the stipes proper. In fact, it would appear from a comparison with the structures of certain Crustacea, that the parastipes, "pas," originally was a part of the basal segment or cardo, and become secondarily united with the stipes, but it is simpler to treat of the parastipes as a portion of the stipes.

In a paper which will be published in the 1921 volume of the Proceedings of the Ent. Society of Washington, it has been pointed out that the maxilla of a larval neuropteron such as the one shown in Fig. 23, corresponds in a remarkable fashion to the typical crustacean limb represented by the maxilliped of *Gammarus* (an amphipodan crustacean) for example, since in both cases, the mouthpart-limb is composed of seven segments, and the correspondence in the relative sizes of the individual segments, and the processes they bear, is marvellously close, when one takes into consideration the fact that we are dealing with forms belonging to distinct classes of arthropods. Such a comparison of the parts in insects and Crustacea very clearly demonstrates that the basal segment or cardo, "car," of Fig. 23 represents the basal segment, or coxopodite, of a crustacean limb. The second segment, or stipes, "bs," of Fig. 23, which bears a median process, "la," (the lacinia) in the insect there figured, clearly corresponds to the second segment or basipodite which also bears a median process or endite in a crustacean mouthpart-limb. The third segment, or palpifer, "ds," of Fig. 23, which bears a median process, "ga," (the galea), evidently corresponds to the third segment or ischiopodite, which also bears a median process or endite in the crustacean mouthpart-limb. The four segments of the maxillary palpus, "mp," of Fig. 23, correspond (even to the relative lengths of the component segment) very closely to the four segments of the endopodite of the maxilliped or *Gammarus*, and there can be no doubt that the maxillary palpus of an insect's maxillary appendage corresponds to the endopodite of a crustacean limb, while the palpifer

with its endite (the galea) and the stipes, with its endite (the lacinia) correspond to the third and second segments of a crustacean mouthpart limb (which also bear endites in *Gammarus*' maxilliped), and the cardo corresponds to the basal segment of such a crustacean mouthpart-limb.

A *basistipes*, "pst," is demarked in the basal region of the stipes, "sti," of the Dermapteron shown in Fig. 7, and if one compares the entire stipes region, bearing the labels "eus" and "pas" in Fig. 10, of a blattid, with the region labeled "pst" in Fig. 7, it should be clear to anyone that the small basal area, "pst," of Fig. 7 is not the entire stipital region "eus" and "pas" of Fig. 10—which may be taken as the basis for comparison with the higher forms. Similarly, when one compares the maxilla of a primitive Coleopteron, such as that shown in Fig. 4, with the maxilla of the Dermapteron (earwig) shown in Fig. 7, it should be perfectly evident that the latero-basal area, "pst" of the stipes of the beetles maxilla (Fig. 4) is in every way homologous with the latero-basal area, "pst," of the stipes of the earwig's maxilla (Fig. 7). On this account, it is quite incorrect to term the area "pst" the "stipes" in beetles (Figs. 4, 3, etc.), as is done by coleopterists in general. In fact, if one compares the maxilla of the beetles shown in Figs 4, etc., with that of the beetle shown in Fig. 1, in which the stipes, "sti," is retained in a condition more nearly approaching that typical of the lower insects, it is at once apparent that the small area, "pst," of the beetle shown in Fig. 4 cannot possibly be homologized with the entire area, "sti," of the beetle shown in Fig. 1, and since the area "pst" of Fig. 4 evidently represents a basal subdivision of the entire stipes, it has been referred to as the basistipes in the present paper. A basistipes, "pst," is demarked from the stipial region only in certain Coleoptera (Fig. 4) and Dermaptera (Fig. 7) so far as I am aware, and the presence of this peculiar subdivision of the stipes in the Coleoptera and Dermaptera alone, would add further support to the view that the Coleoptera are extremely closely related to the Dermaptera—which is borne out by the study of numerous other structural details as well.

In the Dermapteron shown in Fig. 7, the *palpifer*, "pfr," is clearly demarked from the stipes, but the palpifer is not closely associated with the galea, "dg," in this insect, as is the case with the larva shown in Fig. 23. On the other hand, if one compares the larval Neuropteron shown in Fig. 23, with the larval Coleopteron shown in Fig. 27, it will be noted that the palparium or palpifer, "ds," which bears the galea, "ga," is slender, and resembles a basal segment of the palpus in both of these insects, thus adding further support to the view that the Coleoptera are very closely related to the Neuroptera (as well as to the Dermaptera). The Coleoptera are anatomically intermediate between the Dermaptera on the one side and the Neuroptera on the other, and, strange to say, an adult Coleopteron is, as a rule, more like a Dermapteron in structure than it is like a Neuropteron, while a larval Coleopteron is usually more like a larval Neuropteron in structure (although in some features larval Coleoptera are very like immature Dermaptera also).

In the Neuropteron shown in Fig. 86, the palpifer is adherent to the stipes, while in the Mecopteron shown in Fig. 85, it is less closely associated with the stipes, and in the Mecopteron shown in Fig. 84 it has the appearance of a basal segment of the maxillary palpus, "mp." I am not sure of this interpretation, however, since the structure interpreted as the palpifer may actually be a basal segment of the palpus, and on this account no label was affixed to the structure in question. In the beetle shown in Fig. 3, the palpifer, "pfr," is much larger than in most Coleoptera (Figs. 1, 3, etc.); it has also developed a peculiar prominent *palpiferal angle* or projecting angle-like process in the region bearing the label "pfr," and through a distortion or shifting of the parts, the maxillary palpus, "mp," comes to lie over the surface of the palpifer in a peculiar fashion.

I had at first considered that the areas labeled "bs," "in" and "ds" in Fig. 25, for example, represent three divisions of the stipes (i. e., basistipes, interstipes and dististipes) and therefore affixed to these areas labels indicating that they are divisions of the stipes. After the blocks for the plates had been made, however, and it was therefore too late to change the labelling, a further study of the palpiferal region brought to light considerable evidence for considering that the sclerite labeled "ds" in Fig. 25 represents the true palpifer or palparium, and is therefore not a part of the stipes. The area bearing the label "bs" in Fig. 25, however, is apparently a *proxistipes*, or proximal subdivision of the stipes, and the area labeled "in" is apparently a *dististipes*, or distal subdivision of the stipes. In Figs. 31, 23, 27, 22, 21, 20, 24 and 26, on the other hand, the sclerite labeled "bs" apparently represents the entire stipes, rather than a proximal subdivision of the stipes, as the label indicates, while the sclerite labeled "ds" in these figures apparently represents the true palpifer instead of a distal subdivision of the stipes, as the labels indicate. It thus comes about that the label "bs" indicates a basal subdivision of the stipes in Figs. 25, etc., but in the other figures mentioned above, the label "bs" indicates the entire stipes, but I have been unable to change the labeling in the plates to indicate this fact.

In the sawfly larvæ shown in Fig. 49 and 54, a narrow marginal region bearing the label "gg," bearing the galea "ga" is demarked by a well defined suture. The area labeled "gg" in these figures may represent the palpifer, since it bears the galea—as is true of the palpifer in Fig. 23, etc. If this be correct, the sclerite labeled "pfr" in Figs. 49 and 54, is merely a modified basal segment if the maxillary palpus, "mp," instead of representing the palpifer as indicated by the label. Provisionally, however, I have followed the customary usage of hymenopterists in referring to the sclerite labeled "pfr" in Figs. 49 and 54, as the "palpifer." In the sawfly larva shown in Fig. 30, the so-called palpifer, "pfr," curves outward and forward to form the peculiar *palpiferal process*, while the stipes extends laterally in the *stipital angle* or *process*, bearing the label "sa." There is also a small *cardine angle*, "ca," in the sawfly shown in Fig. 30; and the peculiar processes

and angles formed by the parts of the maxillæ in the sawfly larvæ may offer points of value in their classification.

The *galea* is divided into a basal segment, or *basigalea*, "bg," and a distal segment, or *distigalea*, "dg," in the sawfly larvæ shown in Figs. 54 and 49, as is also the case with the galea "ga" of the larvæ shown in Figs. 20, 22, etc. These segments of the galea are apparently homologous with the two segments of the galea, "ga," of the beetle shown in Fig. 3, and with the structures labeled "bg" and "dg" in lower insects (Figs. 10 and 7). These parts of the galea were designated as the basigalea and distigalea in a paper dealing with the maxillæ of Orthoptera (Crampton, 1916); but Yuasa, 1920, in his paper on the mouthparts of the Orthoptera has substituted a terminology of his own for the parts in question. Since the designations originally applied to the parts are as suitable as those which Yuasa has attempted to substitute for them, the original terminology has been retained in the present paper.

Since the galea, "ga," of the larva of *Corydalis* (Figs. 15 and 14) is not like that of the adult ("ga" of Fig. 11) in appearance, and since the lacinia, "la," of an adult *Corydalis* (Fig. 11) cannot be readily detected in the larval stages (Fig. 15), there might be some doubt as to the interpretation of the parts in the larva and adult. I have therefore included Dr. Craighead's figures of the musculature of an adult and larval *Corydalis* (Figs. 11 and 14) in order to show that practically the same muscles occur in both stages (so far as the type of muscle is concerned) and furnish an excellent means of determining the homologies of the parts. As is shown in Dr. Craighead's figures, the tentoriocardine muscles labeled "3" and "4" in Figs. 11 and 14 extend from the tentorium to the cardo in both adult and larval stages of *Corydalis*, and the same paragula-cardine muscles bearing the label "5" extend from the paragular region to the cardo in both larval and adult head. Dr. Craighead states that "the cardo always articulates to the hypostoma and carries at least two muscles, one (number 3) attaching it to the tentorium, and the other (number 5) attaching it to the epicranium."

The tentorio-stipital muscle labeled "2" and the paragula-stipital muscle labeled "6" connect the tentorium and paragular region with the base of the stipes in both stages. With regard to the muscles to the galea and maxillary palpus, Dr. Craighead states that "the upper limit of the stipes, or more correctly, the insertion of its appendages, the galea and lacinia, is indicated by muscles "7" and "8," one attached to the base of the galea, the other to the basal joint of the palpi or palpifer and extending to the base of the stipes, or occasionally one may go to the cardo or a part of it may extend down further to the tentorium." It is quite apparent that muscles "7" and "8" are the same in both adult (Fig. 11) and larva (Fig. 14) of *Corydalis*, so that the structure labeled "ga" in Fig. 14 must be the homologue of the galea "ga" (Fig. 11) of the adult insect, since the same stipito-galeal muscle "7" is attached to the structure labeled "ga" in both larva and adult. The lacinia, "la," of the adult (Fig. 11) is apparently wanting in the larva (Fig. 14) of *Corydalis*, and Dr. Craighead states that "it (the lacinia) is considered to be lacking in most coleopterous larvæ. However, in

certain larvæ two lobes appear, and, as far as I know, only one carries muscles." (The lacinia, "la," of Fig. 11 is thought by Dr. Craighead to carry no muscles, thus resembling the inner lobe of the maxilla of the larval Coleoptera, in this respect). He also states that "in certain forms there are indications pointing toward a maxilla with only lacinia or only galea present." In this connection, it may be remarked that the tentorio-labiostipital and tentorio-palpigeral muscles labeled "9" and "10" in Figs 11 and 14, as well as the submento-mental muscles labeled "11" in these figures are the same in adult and larva of *Corydalis*, so that all of the important parts of the trophi (with the exception of the maxillary lacinia) of an adult *Corydalis* are represented in its larva.

Although there is a slight difference between the mouthparts of an adult and larval *Corydalis*, as was mentioned above, the mouthparts are essentially the same in both larva and adult of the lower Neuroptera (*Corydalis*, *Sialis*, *Raphidia*, etc.), the resemblance between the mouthparts of the two stages being very marked in *Raphidia* (a larva of which is shown in Fig. 12), thus indicating a much feebler tendency toward complete metamosphosis in lower Neuroptera. When we turn to the larvæ of the higher Neuroptera, however, we find a much stronger tendency toward complete metamorphosis, and the mouthparts for the most part have become so greatly modified in adaptation to the "larval" methods of getting food, etc., (most of these larvæ suck the blood of their prey) that it is very difficult to determine the interpretation of the terminal portions of the maxillæ, and until suitable material for dissecting the muscles has been obtained, the interpretation of the homologies of the terminal portions of the maxillæ is largely a matter of guesswork. Dr. Tillyard has suggested to me that the slender terminal portion of the maxilla bearing the label "mx" in the neuropterous larvæ shown in Figs. 46, 44, 51, etc., may represent the lacinia labeled "la" in Fig. 23 of the larva of *Sialis*, and there is much to be said in favor of this view. On the other hand, the structure in question may not represent the lacinia "la" of Fig. 23, but may rather be homologous with the galea-bearing (or palp bearing) structure labeled "ds" in Fig. 23, with which the galea (or the palp) has fused, and the interpretation of the structures in question can be definitely determined only when material suitable for study has been obtained for an examination of the musculature—although the remarkable larvæ of *Ithone* recently discovered by Dr. Tillyard may throw some light upon this subject.

The *mandible* of an insect represents a single basal segment of a trilobite limb, as can be seen by tracing the development of the mandibular appendage through a series represented by the trilobite *Triarthrus*, the Crustacea *Nebalia*, *Mysis*, *Apseudes*, etc., and the insect *Machilis*—as has been done in a paper soon to be published in the Journal of the N. Y. Ent. Soc., 1921. When one studies such a series, it becomes apparent that the gnathobase region of the basal segment of the trilobites limb becomes differentiated into a biting region and a grinding region as we pass through the series of Crustacea mentioned above, and the biting region become the *incisor region* bearing the "teeth" for cutting food, while the grinding region (which projects quite markedly in some

Crustacea) forms the so-called *mola* or *molar region* in insects, the molar or grinding region of certain coleopterous larvæ being a region of some interest in the classification of the larval forms. In the mandibles of Crustacea, a fringe of flattened seta-like hairs occurs below the incisor region, between the latter and the molar region of the mandible. Some of the flattened seta-like structures fuse to form a movable appendage called the "*lacinia mobilis*" by carcinologists, and some entomologists have thought that a similar "lacinia mobilis" in the mandibles of insects represents the lacinia of an insect's maxilla. The idea that the various parts of the maxilla are repeated in the mandible (proposed by Packard, Smith, and other entomologists), which has received a rather widespread acceptance, is wholly unfounded and misleading, since the mandible represents only one segment (the coxopodite) of a limb, while the body of the maxilla (i. e., the part at the base of the maxillary palpus) is formed of more than one segment of such a limb (i. e., the basipodite and ischiopodite) and the parts are not at all comparable in the mandible and maxilla, since they are formed in different ways in the two structures. Furthermore, the palpus of the mandibular limb is lost in many of the higher Crustacea, and a structure homologous with the mandibular palpus of the Crustacea has not been found in any insects, despite the statement to the contrary made by several persons who have not properly studied the evolution of the mandibular appendage in insects and related Crustacea.

With regard to the portions of the head capsule formed by the mandibular segment, there is a considerable difference of opinion on the part of embryologists in this matter. Thus Riley, 1904, states that a part of the postgena is formed by the pleural region of the mandible, while a portion of the hypopharynx is formed by the sternum of the mandibular segment. Holmgren, 1909, on the other hand, ascribes the "vertex" and genæ to the mandibular segment, in addition to the upper portion of the hypopharynx. It is difficult to believe that the genæ which are situated immediately above the mandibles and bear the mandibles in most insects, are not portions of the mandibular segment, rather than parts of the protocerebral segment to which Riley, 1904, assigns the genæ. I have, therefore, followed Holmgren in ascribing the genæ to the mandibular segment. As far as the *basimandibula* "bmd" of Fig. 39 is concerned, this sclerite is apparently formed by a chitinization of the articulating membrane at the base of the mandible and is not homologous with the trochantin or plate at the base of the leg in the thorax, as Comstock and others have maintained. Since the sclerite "bmd" of Fig. 39 is formed by the chitinization of the basimandibular membrane, or the articulatory membrane at the base of the mandible, it is also a part of the mandibular segment, as Riley, 1904, states, although it is strange that Riley did not also consider that the gena "ge" of Fig. 39, which is so closely associated with the region "bmd" is not also a portion of the mandibular segment.

The mandibles have two principal articulations with the head capsule. The dorsal articulation of the mandible occurs near the postero-lateral angles of the clypeus, and the condyle of the mandible which

articulates with this region is called the *epicondyle*, or dorsal condyle of the mandible. A ventral condyle of the mandible called the *hypocondyle* articulates in an acetabulum or groove of the hypostomal region of the under side of the head. Comstock and Kochi, 1902, use the terms dorsal and ventral articulations of the mandible in the opposite sense from that employed here; but it is more logical to refer to an articulation which is on the dorsal surface of the head as the "dorsal articulation of the mandible," and the articulation which takes place on the ventral surface of the head as the "ventral articulation of the mandible," without reference to any supposed original position of the sclerites involved in these articulations.

The *hypopharynx*, in the broad sense of the term, includes not only the median tongue like organ or *lingua*, which projects from the floor of the mouth cavity, but also the *paragnaths* (called "superlinguæ" and "paraglossæ"), or lobe-like structures on either side of the median tongue, in such insects as *Hemimerus*, immature ephemerids, etc. Since the median tongue-like lingua is usually the only portion of the hypopharynx to be retained in certain insects, the term hypopharynx is usually applied to the lingua alone. The lingua is formed by the sternites of the labial, maxillary and mandibular segments, according to the embryological investigations of Heymons, Holmgren, and others; and a study of the Crustacea would indicate that this view is the correct one, since a ridge which is apparently the forerunner of the lingua of the hypopharynx of insects, is formed in the sternal region of the mouthpart segments of certain Crustacea.

The paragnaths ("superlinguæ") or lobe-like structures on either side of the median tongue or lingua of the hypopharynx of insects are clearly the homologues of the paragnaths of Crustacea, as may be seen by comparing the structures in question of an immature mayfly with the paragnaths of Crustacea such as *Asellus*, various Isopoda, Amphipoda, etc., (see article in Psyche, 1921) so that it is preferable to apply to these structures of insects the term applied to their homologues, the paragnaths, in Crustacea, instead of employing the term "superlinguæ" or the incorrectly applied term "paraglossæ" (which should be restricted to the labial structures of this name) for them. The paragnaths of Crustacea are apparently detached lobes of the first maxillæ which take up a position behind and slightly mesal to the bases of the mandibles in the higher forms; but in *Apus* and other primitive Crustacea, they are evidently lobes of the first maxillæ. It is wholly incorrect to homologize the paragnaths of insects with the first maxillæ (maxillulæ) of Crustacea, and to homologize the first maxillæ of insects with the second maxillæ of Crustacea, as is done by practically all recent investigators, since the paragnaths of insects are in every way homologous with those of Crustacea, and the first maxillæ of insects represent the first maxillæ (not the second maxillæ) of Crustacea, as has been shown in an article in the Transactions of the Entomological Society of London, 1921, and in an article which will shortly appear in the Proc. Ent. Soc. Washington, 1921.

The *tentorium* is apparently formed by three pairs of invaginations, two of which are anterior (a dorsal and ventral anterior pair of invaginations) forming the dorsal and ventral anterior arms of the tentorium, while the posterior ventral pair of invaginations form the posterior ventral arms of the tentorium. These tentorial arms, whose position is marked by the *frontal pits*, *gular pits*, etc., extend internally to the body of the tentorium. The ventral anterior arms of the tentorium may meet and unite to form a plate called the frontal plate of the tentorium by Comstock and Kochi, 1902.

Infoldings of the integument called *implexes* or *endoplicæ* are frequently formed in the different regions of an insect's body, for the attachment of muscles, or for the strengthening of the body wall somewhat after the manner of corrugations in sheets of metal. In the head capsule, however, these internal folds for the most part form ridges for muscle attachment. These have been described under the discussion of the regions of the head capsule in which they occur.

The foregoing description of the parts in insects in general, is offered merely as the basis for a further more detailed discussion of those external features of insect morphology which appear to be of value in determining the phylogeny and interrelationships of the various groups of insects (and their arthropodan relatives), and on this account the modifications occurring in many of the orders have not been treated of in the present paper, since these can be taken up more profitably in a detailed discussion of each group taken separately. The evidence bearing upon the question of the phylogeny or of the interrelationships of the different groups of insects which have been described in the present paper, may be briefly summarized as follows, leaving the more detailed comparison of the parts in the different orders to be discussed later.

Relationships Indicated by the Head Structures.

A comparison of the head structures of the Diptera with those of the Mecoptera would indicate a very close relationship between these two orders. The fact that the labial palpi, "lp," assume the form of fleshy lobes at the end of the labium in the Mecopteron shown in Fig. 84, the fact that the lacinia of the maxilla is lost, and the galea, "ga," is reduced to a short slender structure, and the presence of the sense organ labeled "so" in the maxillary palpus of the scorpion fly shown in Fig. 84, all point to a close relationship to the Dipteron shown in Fig. 83, in which the same tendencies occur, and the sense organ, "so," occurs on exactly the same segment of the maxillary palpus as in the Mecopteron shown in Fig. 84. These facts are in full accord with the evidence of relationship between the Diptera and Mecoptera drawn from the study of the other regions of the body, such as the thoracic terga and wing bases, the genitalia and terminal abdominal structures, etc.

The Mecoptera may, therefore, be regarded as the nearest living representatives of the types ancestral to the Diptera, although it is by no means certain that both Diptera and Mecoptera were not derived from Neuroptera-like ancestors. In fact the latter is even more probable,

since the tendencies present in such Neuroptera as *Nemoptera* (e. g., the reduction of the hind wings to mere ribbon-like structures, suggesting the precursors of the halteres of Diptera, the elongation of the head region and the slender character of the mouthparts, which apparently presage similar tendencies occurring in the Diptera, the nature of the male genitalia, etc., which are somewhat like those of certain Diptera) are those which one finds recurring in many Diptera, and a number of these tendencies are also exhibited by certain Mecoptera. In fact, *Nemoptera* has more features suggestive of affinities with the Mecoptera and the Diptera than any other Neuropteron which I have been able to examine, and it serves as a connecting-link between the Neuroptera on the one side, and the Mecoptera, with the Diptera, on the other. *Nemoptera*, however, is a rather highly specialized Neuropteron, and, since the Mecoptera (and even the Diptera also) have retained certain features (genitalia, etc.) in a more primitive condition than *Nemoptera* has, the probabilities are that the Mecoptera (and Diptera) were derived from a common ancestral type which gave rise both to Nemoptera and to the Mecoptera, etc. Aside from the presence of the ligula, "lg," in *Nemoptera* (Fig. 86) the mouthparts of this insect are apparently even more like the mouthparts of the Mecopteron *Bittacus* (Fig. 85) than they are like the mouthparts of other Neuroptera, as one can see by comparing Fig. 86 of *Nemoptera* with Fig. 81 of a Neuropteron fairly closely related to *Nemoptera*, since the slender columnar structure bearing the labels "sm" and "mn" in Fig. 86 of *Nemoptera* bears a much stronger resemblance to the region bearing these labels in Fig. 85 of the Mecopteron *Bittacus*, than it does to the region bearing these labels in the Neuropteron shown in Fig. 81. Similarly the long slender maxillary galea, "ga," and the slender lacinia, "la," with its peculiar fringe in *Nemoptera* (Fig. 86) resemble the structures bearing the same labels in Bittacus (Fig. 85) much more closely than they do the structures bearing the same labels in the Neuropteron shown in Fig. 81. These and many other features of the body in general indicate a close relationship between *Nemoptera* and the Mecoptera (with the Diptera), and I am convinced that the immediate ancestors of the family to which *Nemoptera* belongs (i. e., the Nemopteridæ) bore a very striking resemblance to the ancestors of the Mecoptera (with the Diptera). At any rate, we must admit that in order to properly interpret the homologies of the mouthparts, etc., of the Mecoptera and related forms, it is necessary to first study these structures in *Nemoptera*, so that there can be no possible objection to regarding *Nemoptera* as a form morphologically annectant between the rest of the Neuroptera and the Mecoptera (with their allies) even though *Nemoptera* itself may not stand in the direct line of descent of the Mecoptera and Diptera.

The Hymenoptera exhibit some very close resemblances to the Neuroptera in the nature of the mouthparts, and I am rather surprised that the points of similarity between the Coleoptera and Hymenoptera found in other structures, are not more evident in the mouthparts, although when more favorable material has been studied, other forms will doubtless be found which exhibit a greater resemblance between

the mouthparts of the two groups. The character of the structures bearing the label "pg" in Fig. 77 of a Hymenopteron is somewhat suggestive of the condition found in the Neuroptera (Fig. 81), and the tendency for the cardo, "car," of Fig. 77 to straighten out in line with the stipes, "sti," occurring in the Hymenoptera is also found in certain Neuroptera. On the other hand, the tendency to lose the lacinia, and the character of the galea, "ga," of the Hymenopteron shown in Fig. 77 are features suggestive of the Mecoptera, such as the one shown in Fig. 84. In fact, the Mecoptera are related to ***both*** Neuroptera and Hymenoptera, and have apparently inherited tendencies from both sources.

In many respects, the Hymenoptera are fully as primitive as the Neuroptera, and in certain features are even more primitive than the Neuroptera (e. g., nature of the genitalia, retention of cerci, etc.), and I am inclined to seek for the types ancestral to the Hymenoptera among the forms related to the Isoptera (with the Psocida and Zoraptera) on the one hand, and to the Coleoptera (with the Dermaptera) on the other. The mouthparts, however, do not furnish as instructive evidence as might be desired, since even in such primitive Hymenoptera as the one shown in Fig. 80, the mouthparts are quite highly modified. Even the larval mouthparts are very disappointing in this respect in the Hymenoptera, since they do not bear a striking resemblance to the mouthparts of any of the larvæ here figured, although one can detect a slight suggestion of affinities with the Coleoptera, on the one side, and with the Lepidoptera on the other. The Mecopteron shown in Fig. 19 is also disappointingly unlike any of the other insects figured, though it has a few features suggestive of affinities with the Trichoptera. It certainly is much more specialized than the primitive Neuroptera studied, and unless Dr. Tillyard can find some Mecopteron larva of a far more primitive character, he is not justified in assuming that the Mecopterous type is more primitive than the Neuropterous one (taking the group as a whole).

The evidence offered by the head structures is in full accord with the former contention (Crampton, 1920) that the Coleoptera are anatomically intermediate between the Dermaptera on the one side and the Neuroptera on the other, and this may have some bearing upon the question of the origin of the Neuroptera. Of the two groups (Coleoptera and Neuroptera) the Coleoptera are clearly the more primitive, with the exception of the feature of the highly modified fore wings. Other very lowly organized insects such as certain Blattidæ have fore wings quite as highly modified as the most primitive Coleoptera, however, and the fore wings of the Dermaptera are even more highly modified than those of the primitive Coleoptera, so that this feature is of no great importance in determining the relative primitiveness of a group of insects as a whole. The occurrence of the peculiar sclerite, "pst," found only in the maxillæ of Coleoptera (Fig. 4) and Dermaptera (Fig. 7), in addition to other features of resemblance in the two groups (e. g., the nature of the antennal segments, the segmentation of the cerci in certain immature Coleoptera and Dermaptera, the character of the thoracic terga, etc.)

indicates a close relationship between the Coleoptera and the Dermaptera. On the other hand, the occurrence in coleopterous and neuropterous larvæ of the peculiar type of maxillæ with both palp, "mp," and slender galea, "ga," borne on a slender segment-like structure, "ds," (see Figs. 23 and 27) in addition to other features of resemblance in the larvæ of the two groups (e. g., nature of the thoracic sclerites, etc.), indicates a close relationship between the Coleoptera and the Neuroptera. In fact, it is extremely difficult to discover any features which will distinguish a larval Coleopteron from a larval Neuropteron in every case, and certain coleopterous larvæ might readily be mistaken for neuropterous larvæ, so great is the similarity between the two groups. The Coleoptera, however, are the more primitive of the two orders (Neuroptera and Coleoptera) and serve to connect the Neuroptera with the insects related to the Dermaptera on the one side and with those related to the Isoptera (with the Zoraptera) on the other. In some respects, the Coleoptera are very like the Embiidæ, particularly in the nature of the head capsule and certain of the mouthparts, as may be seen by comparing Fig. 17 of a beetle with Fig. 18 of an embiid; and the "roots" of the Coleopteron line of development strike down deeply into the group of insects related to the Dermaptera (i. e., the Embiidæ and Plecoptera), some of the coleopterous features being even more primitive than these features in the Dermaptera although the Dermaptera as a whole are much more primitive than the Coleoptera.

The head region of certain Psocidæ (sensu lato) is very like that of some of the Neuroptera (and Hymenoptera also), particularly in the frontal region of the head. The fact that the head region of some Hemiptera (Corixidæ, etc.) overlaps the pronotum is a feature indicating a relationship to the Psocidæ, when taken in conjunction with other resemblances in the head capsule of the two groups (Hemiptera and Psocidæ). The type of head found in the Psocidæ was apparently derived from the Zorapteron type, which in turn was derived from a Plecopteron type (although the Zoraptera are undoubtedly related to the Isoptera as well). From the morphological standpoint alone, the line of development of the Hemiptera would therefore be suggested by the series Plecoptera, Zoraptera, Psocidæ, Homoptera (the Psyllidæ approach the Psocidæ in many respects) and Hemiptera. The Thysanoptera also approach the Psocidæ in many respects, and I have found a psocid whose head is very suggestive of the type leading to the Thysanopteron type, as will be brought out in a later publication. Not only does the typical psocid head approach the Neuropteron type in many respects, but the head of a sawfly also resembles both of these types very markedly and the evidence offered by a study of the head structures is quite in accord with the former contention (Crampton, 1920) that the Hymenoptera are anatomically intermediate between the Psocidæ and the Neuroptera.

The Head Capsule of the Neuroptera.

Since the Neuroptera are an extremely important group from the standpoint of the study of the phylogeny of the higher insects, I have drawn as many types of neuropterous heads as I have been able to examine, in order that anyone wishing to find out what modifications of the head capsule are to be found in the group, may be able to determine which families give indications of being of value for a phylogenetic study. Furthermore, although a study of the head region alone is of no great value in determining the interrelationships of the members of the order Neuroptera, there are certain features of the head region which offer indications of relationship between certain insects, and the evidence of the head region should be added to that drawn from the study of other parts of the body, in attempting to determine the interrelationships of the families of Neuroptera.

The character of the mouthparts of the larval *Sialis* shown in Fig. 23 would indicate that *Sialis* is as primitive as any of the Neuroptera, and the head capsule in general (Fig. 40) of the larva is as primitive as any. The secondary marking off of the areas labeled "pcl" on either side of the clypeus of the larvæ of *Raphidia* and *Corydalis* (Figs. 41 and 42) represents a higher degree of specialization than is exhibited by the larva of Sialis (Fig. 40). On the other hand, the nature of the occipital region, "ocp," in the head region of the larvæ of Raphida and Corydalis (Figs. 41 and 42) in addition to the presence of the peculiar sclerites, "pcl," in these larvæ indicates a rather close relationship between the two, and the line of development of the Rhaphididæ and Corydalidæ apparently quickly merge as we trace them back to that of the *Sialis* type. The head of a *Chauliodes* larva is so like that of a *Corydalis* larva that there is practically no difference between the two, and there can be no doubt that *Chauliodes* is extremely closely related to *Corydalis*. The head capsule of *Chauliodes* (Fig. 34) furnishes an excellent starting point in taking up the study of the head region of the higher Neuroptera, and it is approached by *Polystochoetes* and also by *Oliarces*, *Ithone* and other Ithoniidæ as closely as any other higher forms. *Oliarces*' head is remarkably similar to that of *Ithone*, as may be seen by comparing Fig. 53 with Fig. 52, and there can be no doubt that these two insects belong to the same family (Ithoniidæ) as is also true of *Raphisma*, although Tillyard in his monograph of the Ithoniidæ does not include these insects (Oliarces and Rhapisma) in the family. Furthermore, the head capsule of the Ithoniidæ is remarkably like that of the primitive Lepidoptera and Trichoptera described by Crampton, 1920, and I am convinced that the Lepidoptera and Trichoptera were descended from ancestors very similar to those of the Ithoniidæ.

With regard to the relationships of the Nemopteridæ, which are of great interest from the fact that they approach the Mecoptera and Diptera in many respects, it must be admitted that the adult heads give but few clews as to their nearest relatives. The head structures of the Nemopterid *Croce*, however, have been figured by Imms, 1911, and indicate that the Nemopterid type was probably derived from forms

related to the Ascalaphidæ and Myrmeleonidæ. The head of a larval Ascalaphid (Fig. 47) is extremely similar to that of a larval Myrmeleonid (Fig. 44) and the head of an adult Myrmeleonid such as that shown in Fig. 70 is very like that of *Nymphes* (Fig. 72) even to the presence of the sense organ, "pm," in the labial palpi of both insects, so that the Nymphidæ very probably represent the types ancestral to the Myrmeleonidæ, etc.

The head and mouthparts of Psychopsis (Fig. 46) are somewhat intermediate between the Myrmeleonid type (Fig. 44) and the Hemerobiid type, which is extremely like that of the Chrysopidæ (Fig. 51) and *Psychopsis* may, therefore, be regarded as a connecting link between the two groups. The head of an adult *Psychopsis* (Fig. 71) is very like that of the Myrmeleonid shown in Fig. 70, and so far as the evidence of the head alone is concerned, *Psychopsis* is quite close to the Myrmeleonids in many respects. Whether *Psychopsis* leads back through the Hemerobiid and Chrysopid type to the Ithoniid type of Neuropteron, I cannot say, since the head alone offers insufficient evidence upon which to base one's conclusions in this matter.

The head of *Nothochrysa* (Fig. 66) is extremely like that of *Apochrysa* (Fig. 67), while that of *Euporismus* (Fig. 68) has many features suggestive of affinities with *Stenosmylus* (Fig. 63). *Miodactylus* (Fig. 69) resembles *Stenosmylus* (Fig. 63) on the one hand and *Nymphes* (Fig. 72) or the Myrmeleonids, on the other. *Porismus* (Fig. 65) is quite like *Euporismus* (Fig. 68) in many respects, but also shows some points of resemblance to *Psectra* (Fig. 62). *Psectra* (Fig. 62) is very like *Sisyra* (Fig. 59) and *Climacea* (Fig. 60) also, and *Climacea* in turn bears a resemblance to *Conwenzia* (Fig. 61). *Osmylus* (Fig. 58) is obviously related to the other Osmylidæ, Hemerobiidæ, and Chrysopidæ, but it also bears a resemblance to *Climacea* and *Conwenzia*. *Sisyra, Climacea, Conwenzia* and similar forms were probably derived from ancestors resembling the Ithoniidæ (Figs. 52 and 53), a family which should include the genera *Oliarces* and *Rhapisma*, as well as *Ithone*, although *Oliarces* has never been included in the family (excepting by Crampton, 1920) despite the fact that its head is exactly like that of Ithone (compare Figs. 52* and 53) as is also true of the thoracic sclerites, etc.

Mantispa (Fig. 57) is a very peculiar form, and its affinities cannot be determined from the adult head alone. Its head resembles that of Chrysopa, in some respects, and its closest affinities may be with these insects. On the other hand, the head of *Mantispa* exhibits some similarities to the head of *Nemoptera*, although these resemblances are probably more superficial. The resemblance to the head of *Conwenzia* is more marked, and it is possible that *Mantispa* may be related to both *Chrysopa* and *Conwenzia*.

* Dr. Tillyard has very kindly given me some specimens of *Ithone* preserved in alcohol, and an examination of this material (made after this paper had been prepared) would indicate that the labial region in Figs. 52 and 53 was so distorted as to be quite "unnatural" in the dried specimens from which the drawings were made.

SUMMARY.

The principal structures of the head, the sclerites of the head capsule, and the subdivisions of the mouthparts may be briefly summarized in the following table in which the relations of the parts to one another are also shown.

- Epicranium
  - Occiput — Trophiger
  - Parietals
    - Postcranials
    - Vertex
    - Adfrontals
  - Facies
    - Parafrons
    - Frons
      - Antefrons — Epistoma
      - Postfrons
    - Clypeus
      - Anteclypeus
      - Postclypeus
  - Laterocranium
    - Genæ, with Basimandibula
    - Postgenæ
      - Hypostoma
      - Paragula
- Gulamentum
  - Gula
  - Submentum

Mentum

- Eulabium
  - True labium
    - Labial palpi
    - Palpiger
    - Labiosternite
    - Labiostipes
    - Ligula
      - Glossæ
      - Paraglossæ

- Maxilla
  - Basimaxilla
  - Maxillary palpus
  - Body of maxilla
    - Cardo
      - Eucardo
      - Paracardo — Dististipes
      - Eustipes — Proxistipes
    - Stipes
      - Parastipes — Basistipes
    - Palpifer
    - Galea
    - Lacinia

Mandible

- Labrum
  - Antelabrum
  - Postlabrum

Epipharynx

- Hypopharynx
  - Lingua
  - Paragnaths (parts of maxilla associated with hypopharynx)

Endoplicæ

- Tentorium
  - Body of tentorium
  - Frontal plate of tentorium
  - Dorsal anterior arms
  - Ventral Anterior arms
  - Posterior arms

A study of the embryological development of the head of an insect and a comparison with the head region of the Crustacea (which are like the ancestors of insects) would indicate that six primitive segments enter into the composition of the head of an insect. The protocephalon, antennal, intercalary, mandibular, first maxillary, and second maxillary (labial) segments of an insect's head correspond to the protocephalon, antennular, antennal, mandibular, first maxillary, and second maxillary segments, respectively, in a crustacean's head. The so-called "superlinguæ" of insects are homologous with the paragnaths, not with the "maxillulæ" (first maxillæ) of Crustacea. The mandible of an insect represents only one (the basal) segment of a crustacean's limb, while the body of the maxilla of an insect is composed of several segments of such a limb, so that the parts of an insect's maxilla are not represented in the mandible.

In conjunction with other structures of the body, the head region of insects furnishes indications of a relationship to the Crustacea on the one side, and to the Symphyla on the other. *Machilis* among the Apterygota, and the ephemerids among the Pterygota have retained a number of features suggestive of affinities with the Crustacea, and the head region of *Machilis* would indicate that it is an extremely ancient type related to such forms as *Lepisma Nicoletia*, etc. (and also to *Japyx* and *Campodea*) on the one hand, and to the Collembola on the other. The head of *Machilis*, *Lepisma* and *Nicoletia* among the Apterygota have more suggestions of crustacean affinities, while the head of *Japyx* and *Campodea* is very like that of *Scolopendrella* and other Symphyla-like forms.

Lepisma offers a connecting link between *Machilis* (which leads to the crustacean forms) and the lower winged insects such as the Plecoptera, ephemerids, etc., and the head of immature Plecoptera approach as closely as any type, to that of *Lepisma*. The head of an immature Plecopteron on the other hand, is extremely similar to that of *Arixenia* among the Dermaptera. The head structures of the Dermaptera (and the Embiidæ also) in turn lead to the type found in Coleoptera, particularly in the structure of the maxillæ. As we trace the head types from the Coleoptera upward, the Neuroptera appear to be the next of kin, since the head structures of larval Coleoptera and Neuroptera are astonishingly alike. The Neuroptera

in turn lead to the Mecoptera, Diptera, and Siphonaptera, on the one hand, and to the Trichoptera and Lepidoptera on the other, the neuropterous head which most resembles the head of the Mecoptera and Diptera being that of *Nemoptera*, while the neuropterous head which most resembles that of the Trichoptera (such as *Philopotamus*) and Lepidoptera (such as the micropterygids) is the head of *Oliarces* and other Ithoniidæ.*

The head of a Zorapteron is intermediate between that of certain Plecoptera such as *Capnia*, *Leuctra*, etc., and the Psocid type. Certain of the Psocidæ, in turn, have elongate heads suggestive of affinities with the Thysanoptera, while others exhibit undoubted affinities with the Homoptera and Hemiptera. The head of a mallophagan was undoubtedly derived from the psocid type, and the head structures of the Pediculidæ exhibit affinities with the Mallophaga, etc., as well.

The head structures of Hymenoptera are rather puzzling. They exhibit features suggestive of the Mecoptera on the one side, and with the Neuroptera, as well as the Zoraptera and Psocidæ, on the other. The Psocidæ likewise exhibit certain features very suggestive of a relationship to the Neuroptera, and there is apparently a rather complicated interrelationship between these groups, as is shown in the head structures as well as in other features of the body, such as the ovipositor, etc. In certain respects, the head structures of Hymenoptera (even of the sawflies) are rather highly modified, but the sawfly type is a far more ancient one than it is commonly supposed to be, and probably arose from ancestors intermediate between the Zoraptera (with the Isoptera) on the one side, and the Coleoptera (with the Dermaptera) on the other.

The study of the head and its appendages has shown that these structures are of prime importance for a study of the interrelationships and phylogeny of insects, and before we can arrive at the correct conclusion concerning the evolution of the various orders, and the origin of the Hexapoda, it will be neces-

*The Hemiptera (and Homoptera) are related not only to the Psocidæ, but to the Lepidoptera, Mecoptera, and Neuroptera, as well and exhibit many features suggestive of affinities with the Lepidoptera and Mecoptera. The lines of development of these forms apparently arose at the point where the Neuroptera and Psocidæ began to diverge, and therefore took over in their development, features common to both. Under these conditions it is readily seen that the Lepidoptera may resemble the Psocidæ and Hemiptera (Homoptera) on the one side, and the Neuroptera, etc., on the other, and this fact has not been sufficiently emphasized by students of insectan phylogeny.

sary to make a detailed study of the head, neck plates, thoracic sclerites and appendages, and the terminal abdominal structures, if the results are to be based upon a firm foundation, since any view based upon the study of the wings alone, and not supported by the evidence drawn from the study of other parts of the body as well, can be accepted only with reservation. So far as the study of the origin of insects and their immediate relatives is concerned, I have found the head structures, and the mandibles in particular, to be of the greatest value; and the study of the head structures in the various orders of insects promises to be of equal importance in determining the interrelationships of insects themselves.

BIBLIOGRAPHY.

Berlese—Gli Insetti—Milan, 1909.
Boerner—Mouthparts of Opisthogoneata—Sitz. Ber. Gesell. Naturf. Fr. Berlin, 1903, p. 58.
Chatin—Morphol. Comp. des Pieces Maxillaires, etc., chez les Insectes Broyeurs, Toulouse, 1884; and La Machoire des Insectes—Paris, 1897.
Comstock and **Kochi**—Head of Insects—Amer. Nat., 26, 1902, p. 13.
Crampton—Maxillae of Orthoptera—Psyche, 23, 1916, p. 83; Head of Insects—Ent. News, 28, 1917, p. 398, and Ann. Ent. Soc. America, 10, 1917, p. 337; Neck of Insects—Ann. Ent. Soc. America, 10, 1917, p. 187; Head of Trichoptera and Lepidoptera—Psyche, 27, 1920, p. 23; Ancestry of Insectan Orders—Trans. Ent. Soc. London, 1919, p. 93, Ent. News, 30, 1919, p. 42, and Psyche, 27, 1920, p. 116; Evolution and Interpretation of Parts of Mandible in Insecta and Allied Arthropods—Jour. N. Y. Ent. Soc., 1921; of Superlingulae—Psyche, 1921; of Maxillae—Proc. Ent. Soc. Washington, 1921.
Folsom—Mouthparts of Collembola—Bull. Mus. Comp. Zool., Harvard, 36, No. 5, 1900, p. 87.
Forbes—Structure of Caterpillars—Ann. Ent. Soc. America, 3, 1910, p. 94.
Fracker—Lepidopterous Larvae—Ill. Biol. Monogr. 2, No. 1, 1915, p. 5.
Heymons—Various embryological papers; Embryology of Hemiptera—Nova. Acta. Abh. K. L. C. Deutschen Akad. Naturf. 74, No. 3, p. 353.
Holmgren—Termitenstudien—Kgl. Sv. Vetskakad. Handl., 44, No. 3, p. 3.
Hosford—Head of Insects—Kans. Univ. Sci. Bull. 8, 1913, p. 65.
Janet—Const. Morphol. de la Tete del'Insecte, Paris, 1899.
Kellogg—Mouthparts of Insects—Amer. Nat., 26, 1902, p. 683; Mouthparts of Lepidoptera—Amer. Nat., 5, 1895, p. 546; Mouthparts of Diptera—Psyche, 8, 1899, p. 303, 327, 346, 355, 363.
MacGillivray—Head of Sawfly Larvae—44th Ann. Rept. Ent. Soc. Ontario, 1913, p. 54.
Mangan—Mouthparts of Blattidae—Proc. Roy. Irish Acad. 27, 1908, p. 1.
Packard—Head of Insects—3rd. Rpt. U. S. Ent. Comm., 1882, p. 304; Entomology, 1898.
Peterson—Head of Diptera—Ill. Biol. Monographs, 3, 1916, No. 2.
Riley—Embryology of Head of Blatta—Amer. Nat., 38, 1904, p. 777.
Smith—Mouthparts of Insects—Amer. Phil. Soc., 19, 1896, p. 175; Mouthparts of Diptera—Trans. Amer. Ent. Soc. 17, 1890, p. 319.
Verhoeff—Head of Insects—Nova. Acta. Abh. K. L. C. Deuts. Akad. Naturf. 84, 1904, p. 3.
Waterhouse—Mouthparts of Insects, London, 1895.
Wesche—Papers on Mouthparts of Diptera in Jour. Roy. Micr. Soc., 1902, p. 412; Ibid., 1909, p. 1; Ibid, 1904, p. 28; Trans. Linn. Soc. London, 9, 1906, p. 339; and Jour. Queck. Micr. Club, 1908, p. 283.
Yuasa—Head of Orthoptera and Dermaptera—Jour. Morphol., 33, 1920, p. 251.

ABBREVIATIONS.

ac.....anteclypeus.
af.....adfrons.
anf.....antennifer.
ant.....antennæ.
ap.....labiappendices.
bat.....basantenna.
bg.....basigalea.
bl.....basilacinia.
bm.....basimaxilla.
bmd....basimandibula.
bs.....stipes, or its basal portion.
ca.....cardine angle.
car.....cardo.
cl.....clypeus.
cs.....coronal suture.
dg.....distigalea.
ds.....palparium, or palpifer.
ec.....epicondyle.
eps.....epistoma.
euc.....eucardo.
eus.....eustipes.
f.....laciniafimbrium.
fp.....frontal pits.
fr.....frons.
fs.....frontal suture.
g.....galeafimbrium.
ga.....galea.
ge.....gena.
gg.....galeafer (possibly palpifer).
gl.....glossa.
gp.....gular pits.
gu.....gula.
hc.....hypocondyle.
hs.....hypostoma.
in.....dististipes.
is.....intersternite (postgula).
l.....labrum.
la.....lacinia.
lc.....lacinial cleft.
lg.....ligula.
lp.....labiopalpus (labial palp).
ls.....labiostipes.
m.....myocicatrix.
md.....mandible.
mgs....midgular suture.
mn.....mentum.
mp.....maxillipalpus (maxillary palp).
mx.....maxilla.
oc.....ocelli.
ocp.....occiput.
pa.....parietals.
pac.....paracardo.
pas.....parastipes.
pc.....postclypeus.
pcl.....paraclypeus ("jugum?").
pf.....parafrons.
pfr.....palpifer (in some cases basal segment of palp?).
pg.....paraglossæ.
pgr.....palpiger.
pgu.....paragula.
pm.....palpimacula.
poc.....postorbital crest.
prg.....pregula.
prm....basilabrum (premental plate).
ps.....laterocranial (paracephal) sutures.
pst.....basistipes.
sa.....stipital angle.
sar.....sensarea.
se.....sensorium.
sm.....submentum.
sml.....submentales.
so.....sense organ.
spt.....spinneret.
sti.....stipes.
stm.....stemmata (larval "ocelli").
x.....attachment of stipital plica.

MUSCLES.

1. tentorio-intramaxillary muscle.
2. tentorio-stipital muscle.
3. tentorio-paracardine muscle.
4. tentorio-eucardine muscle.
5. paragulo-cardine muscle.
6. paragulo-stipital muscle.
7. tentorio-galeal muscle.
8. stipito-palpal muscle.
9. tentorio-labiostipital muscle.
10. tentorio-palpigeral muscle.
11. submento-menta' muscles.

EXPLANATION OF PLATES.

(Unless otherwise stated, all Figures are of adult insects).

PLATE II.

Fig. 1. Posterior view of right maxilla of *Chauliognathus marginatus* (Coleoptera).
Fig. 2. Posterior view of right maxilla of *Corydalis cornutus* (Neuroptera).
Fig. 3. Posterior view of right maxilla of *Harpalus* (Coleoptera).
Fig. 4. Posterior view of right maxilla of *Necrophorus* (Coleoptera).
Fig. 5. Posterior view of head of larval Silphid (Coleoptera).
Fig. 6. Posterior view of head of *Gryllus* (Orthoptera).
Fig. 7. Posterior view of head of *Arixenia* (Dermaptera).
Fig. 8. Posterior view of head of larval Pyrochroid (Coleoptera).
Fig. 9. Posterior view of head of larval *Tenebrio* (Coleoptera).
Fig. 10. Posterior view of head of *Periplaneta orientalis* (Blattida).

PLATE III.

Fig. 11. Posterior view of head of *Corydalis* (Neuroptera).
Fig. 12. Posterior view of head of larval *Raphidia* (Neuroptera).
Fig. 13. Posterior view of head of alate *Termopsis* (Isoptera).
Fig. 14. Posterior view of head of larval *Corydalis* (Neuroptera).
Fig. 15. Posterior view of head of larval *Corydalis* (Neuroptera).
Fig. 16. Posterior view of head of *Termopsis* soldier (Isoptera).
Fig. 17. Posterior view of head of *Harpalus* (Coleoptera).
Fig. 18. Posterior view of head of *Embia major* (Embiidina).
Fig. 19. Posterior view of larval *Panorpa* (Mecoptera).

PLASE IV.

Fig. 20. Posterior view of mouthparts of larval *Limnephilid* (Trichoptera).
Fig. 21. Posterior view of mouthparts of larval *Psilotreta* (Trichoptera).
Fig. 22. Posterior view of head of larval Elaterid (Coleoptera).
Fig. 23. Posterior view of mouthparts of larval *Sialis* (Neuroptera).
Fig. 24. Posterior view of mouthparts of larval *Polycentropid* (Trichoptera).
Fig. 25. Posterior view of mouthparts of larval *Prionyxtus* (Lepidoptera).
Fig. 26. Posterior view of mouthparts of larval *Rhyacophila* (Trichoptera).
Fig. 27. Posterior view of head of larval *Hydrophilus* (Coleoptera).
Fig. 28. Posterior view of right maxilla of larval *Schizura concinna* (Lepidoptera).
Fig. 29. Posterior view of head of larval *Achroia grisella* (Lepidoptera).
Fig. 30. Posterior view of mouthparts of larval *Cimbex* (Hymenoptera).
Fig. 31. Posterior view of mouthparts of larval *Hepialus* (Lepidoptera).

PLATE V.

Fig. 32. Frontal view of head of larval *Neurotoma* (Hymenoptera).
Fig. 33. Frontal view of head of *Raphidia* (Neuroptera).
Fig. 34. Frontal view of head of *Chauliodes* (Neuroptera).
Fig. 35. Frontal view of head of *Sialis* (Neuroptera).
Fig. 36. Frontal view of head of *Anisolabis maritima* (Dermaptera).
Fig. 37. Frontal view of head of male *Corydalis* (Neuroptera).
Fig. 38. Dorsal view of head of larval *Chalcophora* (Coleoptera).
Fig. 39. Frontal view of head of alate *Mastotermes darwinensis* (Isoptera).
Fig. 40. Frontal view of head of larval *Sialis* (Neuroptera).
Fig. 41. Frontal view of head of larval *Raphidia* (Neuroptera).
Fig. 42. Frontal view of head of larval *Corydalis* (Neuroptera).

PLATE VI.

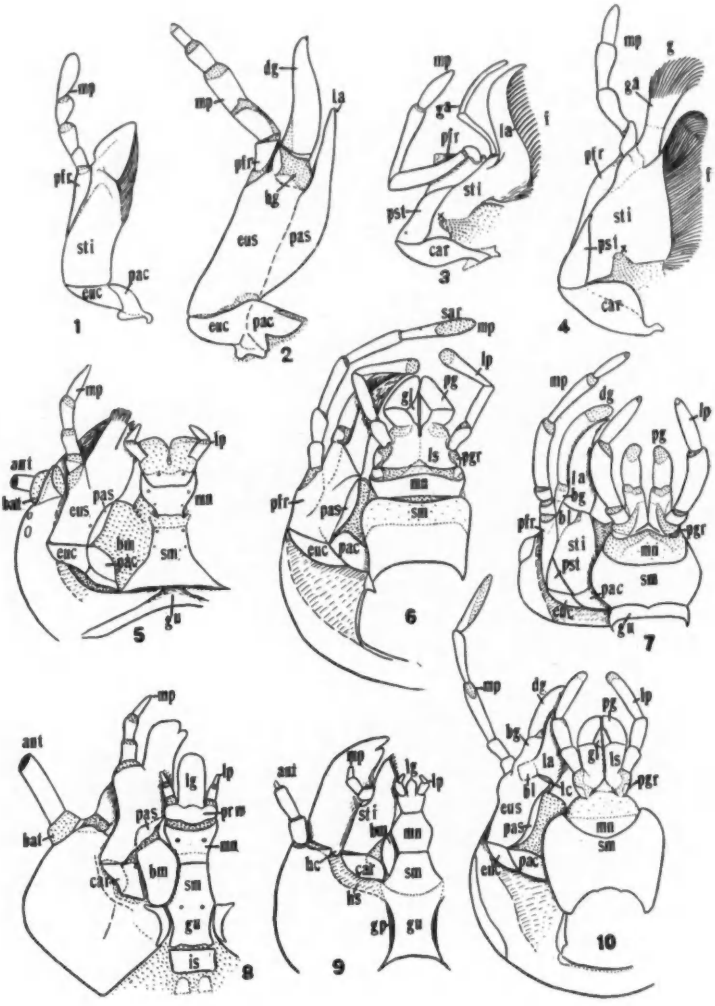
Fig. 43. Frontal view of head of *Berotha piepersii* (Neuroptera).
Fig. 44. Posterior view of mouthparts of larval *Myrmelionid* (Neuroptera).
Fig. 45. Frontal view of head of *Polystochoetes* (Neuroptera).
Fig. 46. Posterior view of mouthparts of larval *Psychopsis elegans* (Neuroptera).
Fig. 47. Posterior view of mouthparts of larval Ascalaphid (Neuroptera).
Fig. 48. Frontal view of head of *Dilar corsicus* (Neuroptera).
Fig. 49. Posterior view of head of larval *Megaxyela* (Hymenoptera).
Fig. 50. Ventral view of head of larval *Climacea* (Neuroptera).
Fig. 51. Posterior view of head of larval Chrysopid (Neuroptera).
Fig. 52. Frontal view of head of *Ithone fusca* (Neuroptera).
Fig. 53. Frontal view of head of *Oliarces clara* (Neuroptera).
Fig. 54. Posterior view of head of larval *Neurotoma* (Hymenoptera).
Fig. 55. Posterior view of head of larval *Cowenzia hageni* (Neuroptera).
Fig. 56. Frontal view of head of *Nemoptera sinuata* (Neuroptera).
Fig. 57. Frontal view of head of *Mantispa pagana* (Neuroptera).

PLATE VII.

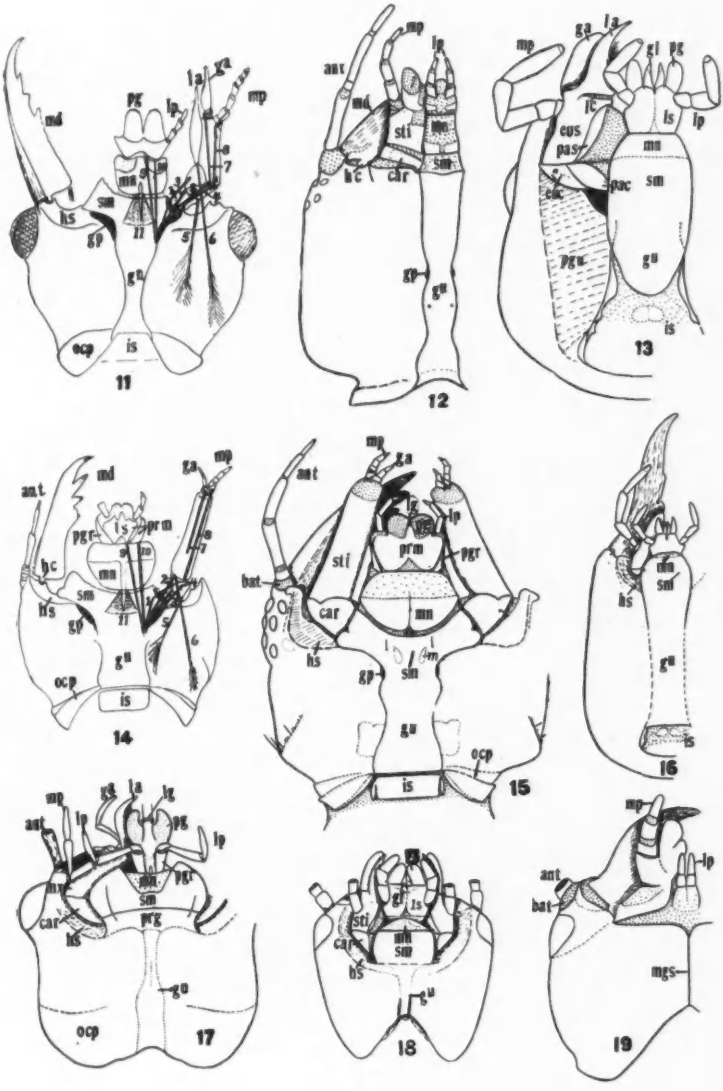
Fig. 58. Frontal view of head of *Osmylus maculatus* (Neuroptera).
Fig. 59. Frontal view of head of *Sisyra* (Neuroptera).
Fig. 60. Frontal view of head of *Climacea* (Neuroptera).
Fig. 61. Frontal view of head of *Conwenzia hageni* (Neuroptera).
Fig. 62. Frontal view of head of *Psectra dipterum* (Neuroptera).
Fig. 63. Frontal view of head of *Stenosmylus tenuis* (Neuroptera).
Fig. 64. Frontal view of head of *Chrysopa perla* (Neuroptera).
Fig. 65. Frontal view of head of *Proismus strigatus* (Neuroptera).
Fig. 66. Frontal view of head of *Nothochrysa evanescens* (Neuroptera).
Fig. 67. Frontal view of head of *Apochrysa bellula* (Neuroptera).
Fig. 68. Frontal view of head of *Euporismus albatrox* (Neuroptera).
Fig. 69. Frontal view of head of *Miodactylus pubescens* (Neuroptera).
Fig. 70. Frontal view of head of *Acanthaclistes americana* (Neuroptera).
Fig. 71. Frontal view of head of *Psychopsis insolens* (Neuroptera).
Fig. 72. Frontal view of head of *Nymphes* (Neuroptera).
Fig. 73. Frontal view of head of *Ululodes* (Neuroptera).
Fig. 74. Frontal view of head of *Stilbopteryx* (Neuroptera).

PLATE VIII.

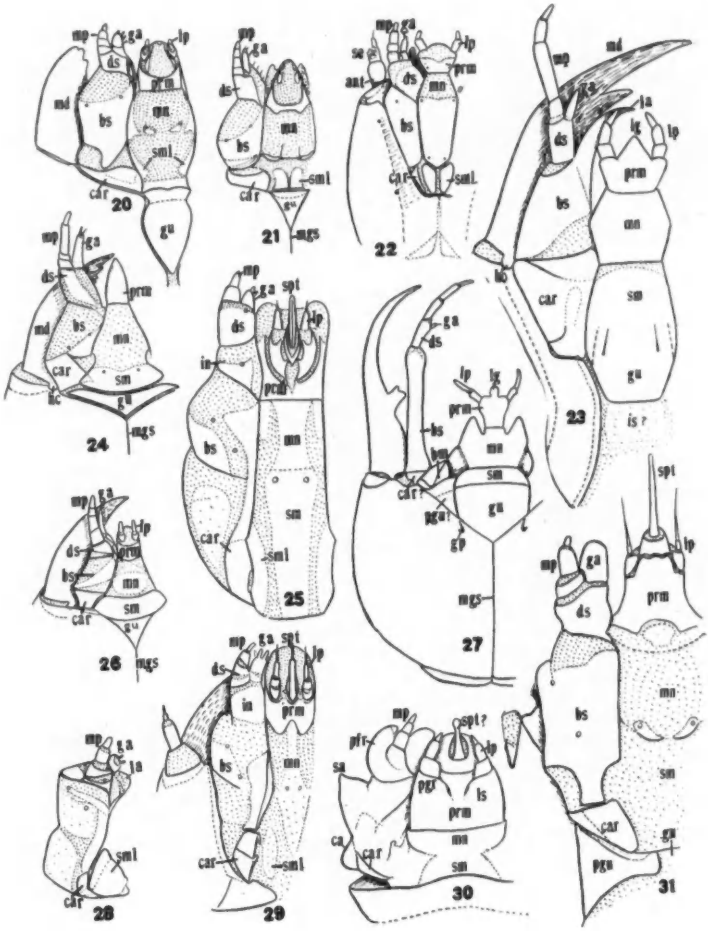
Fig. 75. Posterior view of labium of *Cicada* (Homoptera).
Fig. 76. Lateral view of head of *Belostoma* (Hemiptera).
Fig. 77. Posterior view of mouthparts of *Bracon liberator* (Hymenoptera).
Fig. 78. Frontal view of head of *Macroxyela* (Hymenoptera).
Fig. 79. Frontal view of head of larval *Pyrausta ainsleii* (Lepidoptera).
Fig. 80. Posterior view of mouthparts of *Macroxyela* (Hymenoptera).
Fig. 81. Posterior view of mouthparts of *Nymphes* (Neuroptera).
Fig. 82. Posterior view of labium of *Panorpa lugubris* (Mecoptera).
Fig. 83. Posterior view of mouthparts of *Asyndulum montanum* (Diptera).
Fig. 84. Posterior view of mouthparts of *Nannochorista dipteroides* (Mecoptera).
Fig. 85. Posterior view of mouthparts of *Bittacus* (Mecoptera).
Fig. 86. Posterior view of mouthparts of *Nemoptera sinuata* (Neuroptera).


mp
pfr
sti
pac
euc
1
dg
la
bg
eus
pas
2
pst
car
3
g
f
4
sar
lp
gl
pg
ls
pgr
mn
sm
pas
5
ant
bat
bm
gu
6
7
lg
prm
is
8
9
hc
gp
10

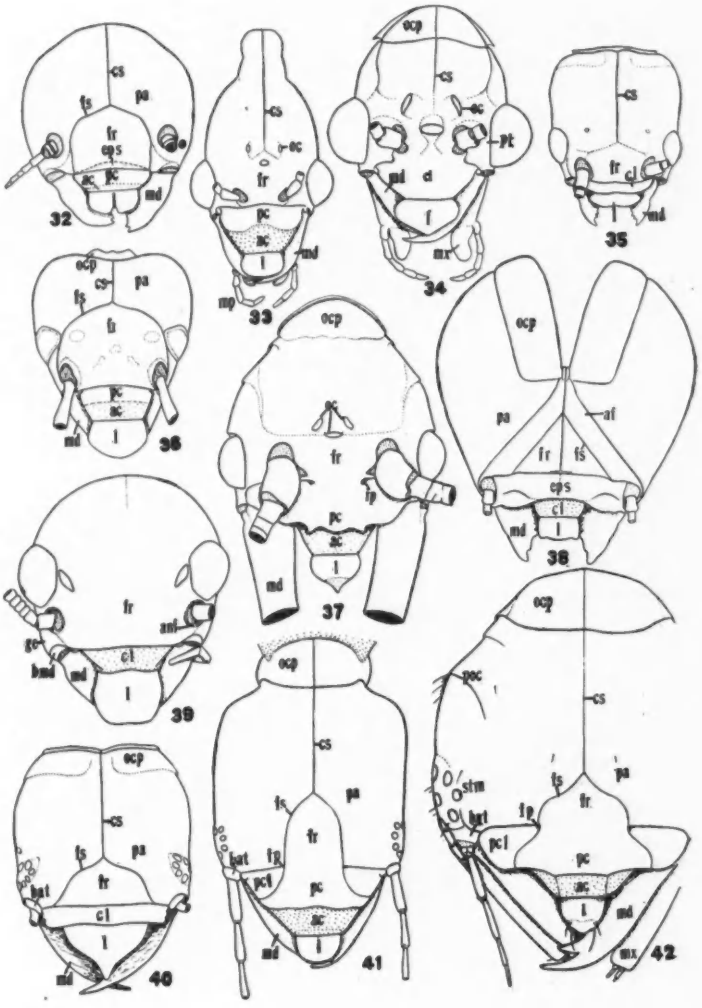
G. C. Crampton.


md
pg
lp
la
ga
mp
hs
sm
gp
gu
ocp
is
11
ant
sti
mn
hc
car
12
gl
ls
eus
pas
pac
pgu
13
prm
pgr
bat
14
15
16
17
18
19
mgs

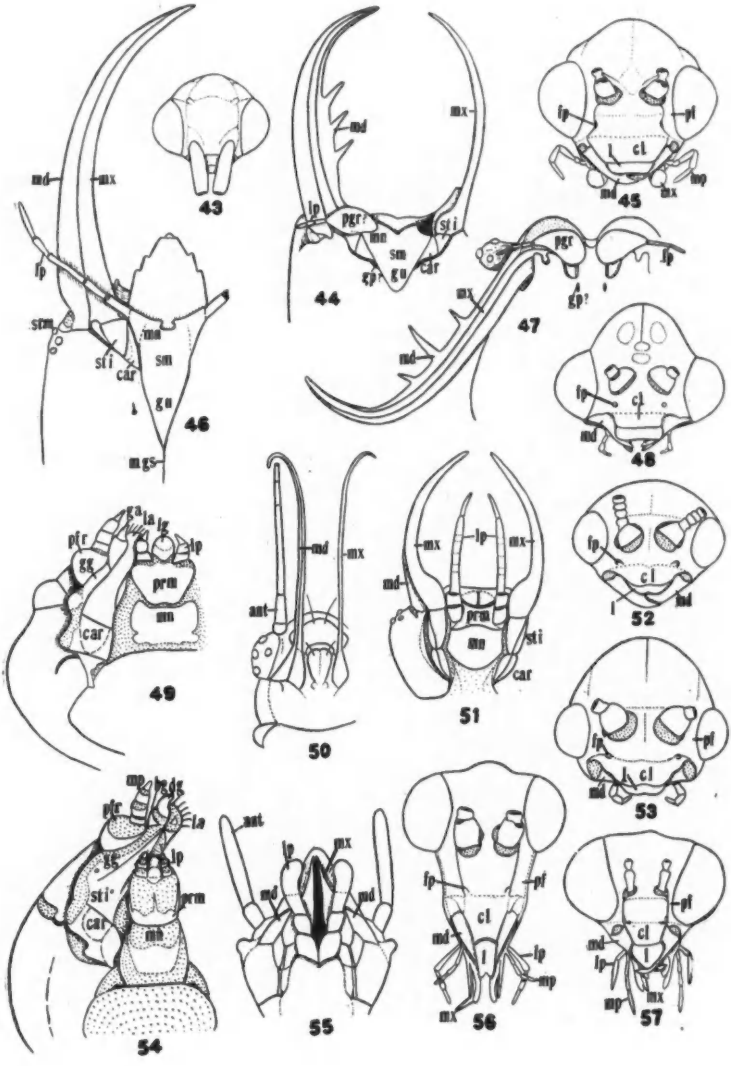
G. C. Crampton.


mp
ga
lp
ds
md
bs
prm
mn
sml
car
gu
20
pp
21
mgs
22
ant
23
24
25
26
27
28
29
30
31
spt
pfr
pgu

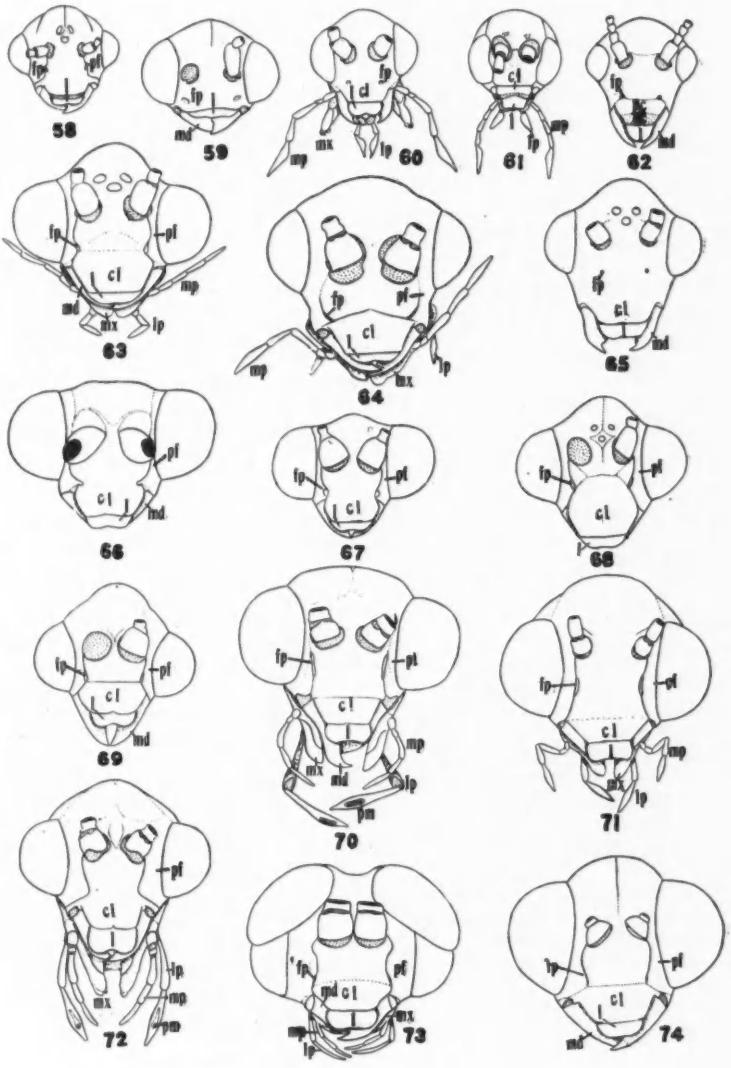
G. C. Crampton.


cs
pa
fs
fr
eps
ac
pc
md
32
oc
33
ocp
pt
mx
34
35
af
cl
l
36
37
38
ant
gc
bmd
39
stm
hat
pcl
40
41
poc
42

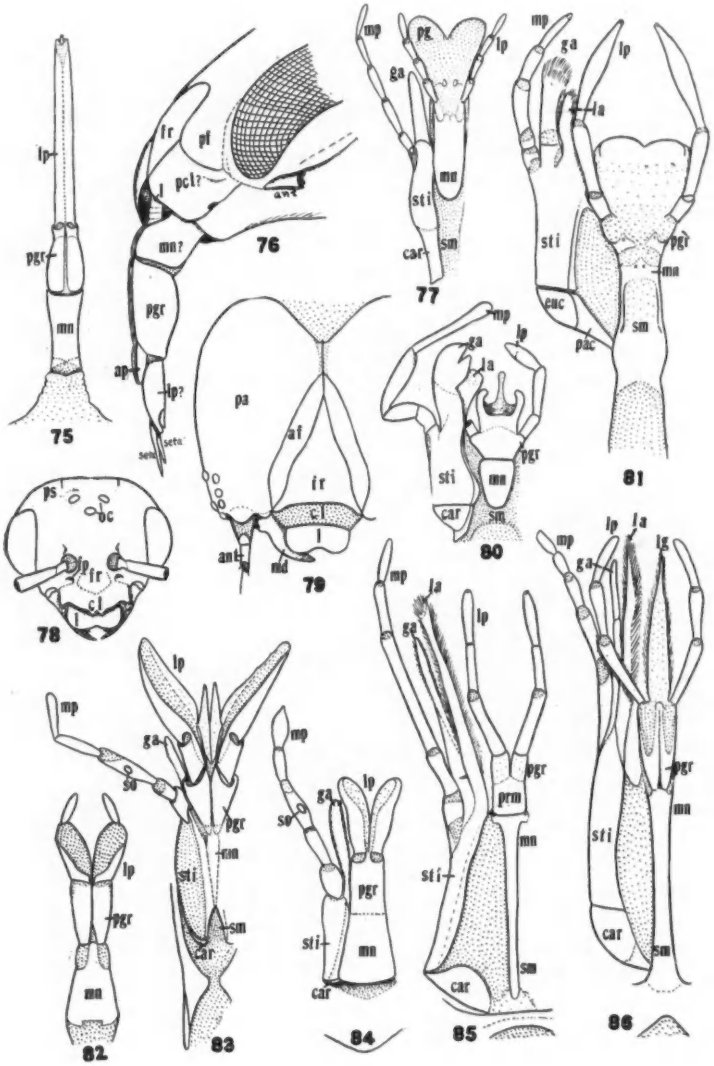
G. C. Crampton.


md
mx
lp
stm
sti
car
sm
gu
mgs
43
46
pgr
mn
gp
44
47
ip
pf
cl
l
mp
45
48
ga
la
lg
pfr
gg
prm
49
ant
50
51
52
53
54
55
56
57

G. C. Crampton.


58
fp
pf
59
fp
md
60
cl
fp
mp
mx
lp
61
cl
fp
mp
62
fp
md
63
fp
pf
cl
mp
md
mx
lp
64
fp
pf
cl
mp
mx
lp
65
fp
cl
md
66
pf
cl
md
67
fp
pf
cl
68
fp
pf
cl
69
fp
pf
cl
md
70
fp
pf
cl
mp
mx
md
lp
pm
71
fp
pf
cl
mp
mx
lp
72
pf
cl
lp
mx
mp
pm
73
fp
pf
md
cl
mx
mp
lp
74
fp
pf
cl
md

G. C. Crampton.


lp
pgr
mn
75
fr
pf
pcl?
ant
mn?
76
pgr
ap
lp?
seta
mp
pg
lp
ga
mn
sti
car
sm
77
mp
ga
lp
la
sti
pgr
mn
euc
pac
sm
81
pa
af
fr
cl
ant
md
79
mp
lp
ga
la
sti
pgr
mn
car
sm
80
ps
oc
lp
fr
cl
78
mp
ga
so
lp
pgr
mn
sti
sm
car
83
lp
pgr
mn
82
mp
ga
so
lp
pgr
sti
mn
car
84
mp
la
ga
lp
pgr
prm
mn
sti
sm
car
85
mp
lp
la
lg
ga
pgr
mn
sti
car
sm
86

G. C. Crampton.

UNDESCRIBED SPECIES OF JAPANESE CRANE-FLIES (TIPULIDÆ, DIPTERA).

Part II.

By CHARLES P. ALEXANDER.

The present paper is a continuation of the first part published under this title (Ann. Ent. Soc. Amer., vol. 12, pp. 327-348; 1919). The material upon which this report is based was received from many different sources. Dr. Kuwana has sent material collected in various parts of Honshu by his assistant inspectors, Mr. Tanaka and Mr. Teranishi. Dr. Machida has collected numerous crane-flies in the vicinity of Tokio and near Tamagawa in the province of Saitama. Mr. Takeuchi sent an interesting series from Gifu. Mr. Kuwayama supplied a series of Tipulinæ from Hokkaido, mostly from the immediate vicinity of Sapporo. One additional species was included in extensive collections of exotic crane-flies belonging to the Paris Museum and sent to me for naming by Mons. Séguy. I express my great indebtedness to all of the gentlemen named for this important series of Japanese Tipulidæ. Unless stated otherwise, the types are preserved in the writer's collection.

Limnobia Meigen.

Limnobia tanakai sp. n.

General coloration yellow; pronotum and anterior portion of mesonotal praescutum with a median brown line; antennæ yellow; vertex with a brown crossband; legs yellow, the tips of the femora and tibiæ narrowly dark brown; wings with a yellowish tinge, sparsely variegated with brown; *r* removed from the tip of R_1; basal deflection of Cu_1 before the fork of *M*.

Male—Length, 8 mm.; wing, 8.7 mm. *Female*—Length, 9 mm.; wing, 8.8 mm.

Rostrum and palpi dark brown. Antennæ uniformly pale yellow; flagellar segments with long verticils. Anterior part of vertex yellow with a sparse whitish pubescence; a dark brown band extending across vertex between the posterior margins of eyes; remainder of vertex and occiput obscure yellow.

Pronotum dark brown, passing into yellow on the sides. Mesonotal praescutum reddish yellow, the anterior median area slightly infuscated; remainder of mesonotum light yellow. Pleura reddish yellow. Halteres obscure yellow. Legs with the coxæ and trochanters yellow; femora

yellow, the tips narrowly dark brown; tibiæ obscure yellow, the tips very narrowly dark brown; metatarsi obscure yellow, the tips brown; remainder of tarsi brown. Wings with a strong grayish yellow tinge, clearer yellow in cells *C* and *Sc;* stigma brown; narrow brown clouds at origin of *Rs; Sc_2;* along cord and outer end of cell *1st* M_2 and less distinctly along the other longitudinal veins; veins dark brown, paler in the costal area. Venation: *Sc* long, Sc_2 ending about opposite two-thirds *Rs; Sc_2* much longer than Sc_1; *Rs* angulated and spurred at origin; *r* far from tip of R_1, about one-half the latter; basal deflection of Cu_1 far before the fork of *M*, the distance about one-half of the deflection.

Abdomen obscure yellow; in the male, the hypopygium is more infuscated.

Habitat: Japan. Holotype, ♂, Ikaho, Gumma-Ken, July 7, 1920 (K. Tanaka). Allotopotype, ♀, in copula with the type.

Limnobia tanakai is named in honor of its collector. It is more closely related to *L. stigma* Meigen (Europe) than to any other described Palaearctic species.

Dicranomyia Stephens.

Dicranomyia paupercula sp. n.

Antennal flagellum dark brown; head dusted with gray; mesonotum pale, covered with a sparse yellow pollen; wings with a faint yellowish tinge; *Sc* short, Sc_2 apparently lacking.

Male—Length about 4.5 mm.; wing 4.6 mm.

Rostrum brown, dusted with gray; palpi obscure brownish yellow. Antennæ with the scapal segments brown; flagellum dark brownish black; flagellar segments oval. Head dark, dusted with gray.

Mesonotum pale with a sparse yellow pollen, without darker markings; scutellum and postnotum sparsely pruinose. Pleura with a yellowish gray pollen, becoming more yellowish on the mesosternum. Halteres pale, the knobs darker. Legs with the coxæ and trochanters concolorous with the pleura; remainder of the legs yellowish testaceous, the tarsi slightly darker. Wings with a faint yellowish tinge, the stigma entirely lacking; veins pale. Venation: *Sc* short, Sc_2 apparently entirely lacking; *Rs* nearly twice the deflection of R_{4+5}; cell *1st* M_2 closed, about as long as the outer section of Cu_1; basal deflection of Cu_1 at or slightly before the fork of *M*.

Abdominal tergites light brown, the sternites brownish yellow.

Habitat: Japan. Holotype, ♂, Koiwai Farm, near Morioka, September 2, 1920 (C. Teranishi).

Dicranomyia paupercula is allied to *D. depauperata* Alex., but is much smaller and with the details of coloration distinct.

Dicranomyia machidai sp. n.

General coloration brownish yellow, the mesonotum marked with darker; a broad, longitudinal dark brown stripe on pleura; antennæ entirely dark; wings brown, stigma oval, dark brown; *Sc* long, Sc_2 at tip of Sc_1; cell *1st* M_2 closed; abdominal tergites dark brown, sternites indistinctly bicolorous; male hypopygium with a single pleural appendage, the terminal beak unprovided with spines.

Male—Length, about 5 mm.; wing, 6.5 mm. *Female*—Length, 6.6 mm.; wing, 5.5–7.2 mm.

Rostrum and palpi dark brownish black. Antennæ dark brownish black throughout; flagellar segments cylindrical, each with a short pedicel. Head dark brownish gray.

Pronotum dark brown, the lateral margins of the scutellum obscure yellow. Mesonotal praescutum brownish yellow with a broad, dorsomedian darker brown stripe that is greatly widened before the suture; lateral margins of praescutum narrowly infuscated; scutal lobes dark brown, the median area obscure yellow; scutellum and postnotum dark brown. Pleura obscure yellow with a very broad and conspicuous dark brown longitudinal stripe extending from the cervical sclerites to the base of the abdomen, passing immediately beneath the halteres; dorsal pleurites darker than the ventral sclerites; mesosternum a little darkened. Halteres dark brown, the base of the stem more yellowish. Legs with coxæ and trochanters yellowish; remainder of the legs brown. Wings with a strong brownish tinge; stigma oval, darker brown; very indistinct seams along the cord and outer end of cell *1st* M_2; veins dark brown. Venation: *Sc* long, Sc_1 extending to about opposite one-half the length of *Rs*, Sc_2 at its tip; *Rs* long, arcuated to feebly angulate at origin; *r* at tip of R_1; basal deflection of R_{4+5} almost straight; cell *1st* M_2 elongate rectangular, subequal to or a little shorter than the ultimate section of M_{1+2}; basal deflection of Cu_1 beyond the fork of *M*; Cu_2 a little shorter than the deflection of Cu_1; vein *2nd A* slightly extended.

Abdominal tergites dark brown; sternites with the basal half of the segments yellowish, the apices dark brown; genital segment in the female brighter. Male hypopygium with the pleurites relatively slender, with a conspicuous fleshy lobe on the proximal face; a single pleural appendage, the tip of which is produced into a curved chitinized beak that bears a few delicate bristles near its apex, but is unarmed with spines. Gonapophyses flattened, broad-based, suddenly narrowed to the slender apex, this latter with a blunt blackened tubercle on the outer side some distance before the tip.

Habitat: Japan. Holotype, ♂, Nakano, May 28, 1920 (H. Machida). Allotype, ♀, Shibuya, October 12, 1920 (H. Machida). Paratopotype, ♀; paratypes, 5 ♂ ♀, Shibuya, June 24-September 29, 1920.

This interesting and very distinct *Dicranomyia* is named in honor of its collector, Dr. Hachiro Machida.

Dicranomyia unispinosa sp. n.

General coloration light brown; antennæ dark brown; wings with a strong brownish tinge; stigma oval, dark brown; *Sc* long; basal deflection of R_{4+5} arcuated; abdomen dark brown; male hypopygium with two pleural appendages; inner face of the ventral pleural appendage with a fleshy lobe that bears a single long spine before its tip.

Male—Length about 4 mm.; wing, 4.3 mm.

Rostrum and palpi dark brown. Antennæ moderately elongate for a member of this genus, if bent backward extending beyond the base of the abdomen; dark brown, flagellar segments suboval, covered with a dense white pubescence. Head dark brown, the anterior part sparsely pruinose.

Mesonotum light brown without distinct darker stripes or other markings. Pleura testaceous, the dorsal region very slightly darker. Halteres testaceous, the knobs brown. Legs with the coxæ and trochanters testaceous, concolorous with the ventral sclerites of the pleura; remainder of legs dark brown. Wings with a strong brownish tinge; stigma oval, darker brown; veins dark brown. Venation: *Sc* long, Sc_1 ending about opposite two-fifths the long *Rs*, Sc_2 at tip of Sc_1; *Rs* long, gently angulated near base, in alignment with R_{2+3}; tip of R_1 and *r* pale, subobsolete; basal deflection of R_{4+5} strongly arcuated; inner end of cell *1st* M_2 gently arcuated; basal deflection of Cu_1 immediately before the fork of *M*.

Abdomen dark brown. Male hypopygium with the pleurites stout, provided with a large, conspicuous lobe on the proximal face; two pleural appendages; dorsal hook straight basally, gently curved on the outer half, the tip acute; ventral pleural appendage a large fleshy lobe whose proximal face near the base is produced into a fleshy rostrum that narrows gradually to the blunt apex; far before the tip on the caudal or outer face a single powerful spine that is about as long as the fleshy tip beyond it. Gonapophyses appearing as broad-based flattened plates that gradually narrow to the apices, the latter slender, with the tips feebly notched. Penis-guard slightly shorter than the apophyses.

Habitat: Japan. Holotype, ♂, Gifu, October 9, 1920 (K. Takeuchi).

Dicranomyia unispinosa bears a strong superficial resemblance to *D. machidai*, but is readily distinguished by the very different structure of the male hypopygium and other smaller characters.

Geranomyia Haliday.

Geranomyia (Geranomyia) gifuensis sp. n.

General coloration light gray; rostrum and antennæ dark brown; humeral angles of praescutum testaceous yellow; pleura yellowish; legs dark brown; wings gray, stigma oval, dark brown; very narrow

seams along the cord and outer end of cell *1st* M_2; *Sc* long; cell *1st* M_2 long and narrow.

Female—Length (excluding rostrum), 6.6 mm.; wing, 7.8 mm.; rostrum alone, 3–3.5 mm.

Rostrum and palpi black. Antennæ black; flagellar segments cylindrical. Anterior part of the vertex light gray pruinose; remainder of the head dark brown.

Pronotum brown medially, gray pruinose. Mesonotal praescutum brown with a conspicuous light gray bloom, the interspaces darker; humeral angles light testaceous yellow to flesh color, this color continued around the anterior margin of the praescutum as a narrow seam; lateral margins of the praescutum caudad of the pseudosutural foveæ dark brown; scutum light gray, the proximal edge of the lobes with a longitudinal dark line; scutellum brownish testaceous, gray pruinose; postnotum dark, gray pruinose. Pleura testaceous yellow anteriorly, sparsely pruinose, especially on the posterior pleurites. Halteres yellow, the knobs and outer end of the stem dark brown. Legs with the coxæ and trochanters yellowish testaceous; remainder of the legs dark brown, bases of the femora paler. Wings with a gray tinge; stigma oval, dark brown; very narrow and indistinct brown seams at the supernumerary crossvein in cell *Sc;* origin of *Rs;* Sc_2; along the cord and outer end of cell *1st* M_2; a narrow seam along the wing-apex in cells *2nd* R_1 and R_3; veins dark brown. Venation: *Sc* long, Sc_1 ending about opposite two-thirds *Rs*, Sc_2 at the tip of Sc_2 deflection of R_{2+3} shorter than the basal deflection of Cu_1; cell *1st* M_2 long and narrow, rectangular, slightly widened outwardly, about as long as vein M_{1+2} beyond it; basal deflection of Cu_1 before or beyond the fork of *M*.

Abdominal tergites dark brown, sternites paler brownish testaceous. Ovipositor reddish horn-color.

Habitat: Japan. Holotype, ♀, Gifu, October 10, 1920 (K. Takeuchi). Paratopotype, ♀.

Erioptera Meigen.

Erioptera (Erioptera) dictenidia sp. n.

General coloration brown, the thoracic pleura gray; femora brownish yellow with a narrow brown subterminal ring; wings faintly brownish; a narrow and very indistinct brown seam along the cord; male hypopygium with the outer pleural appendage stout, chitinized, the apex densely set with parallel rows of small chitinized spinules; inner pleural appendage pale, an acute point on cephalic margin at about two-thirds the length; gonapophyses two, appearing as flattened blades, the outer margin with a comb of about a dozen teeth.

Male—Length about 3.8 mm.; wing, 4.5 mm. *Female*—Length about 4.5 mm.; wing, 5.7 mm.

Rostrum obscure brownish yellow; palpi dark brown. Antennæ dark brown. Head dark gray, paler adjoining the eyes.

Pronotum pale laterally. Mesonotum uniformly light brown, the dorso-median area darker. Pleura light gray pruinose. Halteres pale, the knobs and apices of stem dark brown. Legs with the coxæ concolorous with pleura; trochanters obscure yellow; femora brownish yellow, a narrow dark brown subterminal ring; tibiæ and tarsi obscure brownish yellow, the latter darkened towards the tip. Wings with a faint brown tinge; a narrow and very indistinct brown seam along the cord; veins dark brown. Venation: Vein *2nd A* only moderately sinuous, the distal quarter bent towards the *1st Anal* vein.

Abdominal tergites dark brown; sternites obscure brownish yellow; pleurites of male hypopygium obscure reddish brown. Male hypopygium with the pleurites stout, the inner angle produced into a short, stout lobe provided with several setigerous tubercles; outer pleural appendage a large, stout chitinized arm, densely provided with parallel rows of small, chitinized spinules; inner pleural appendage a pale blade with an acute point on the cephalic or inner margin at about two-thirds the length. Gonapophyses two in number, appearing as flattened chitinized blades, the proximal edge straight, the outer edge with a comb of about a dozen small, acute teeth, the outermost tooth largest, chitinized.

Habitat: Japan. Holotype, ♂, Shibuya, August 7, 1920 (H. Machida). Allotopotype, ♀. Paratopotypes, ♀, June 30, 1920; ♂, October 10, 1920. Paratypes, 7 ♂ ♀, Keijo, Corea, September 6, 1920 (K. Doi.)

Erioptera (Erioptera) bicornifer sp. n.

General coloration brown; pleura sparsely gray pruinose; wings pale gray, veins pale brown; male hypopygium with the inner pleural appendage recurved into an elongate point; gonapophyses appearing as two slender curved horns, blackened at their tips.

Male—Length about 3 mm.; wing, 4.2 mm.

Rostrum and palpi dark brown. Antennæ dark brown. Head brown, discolored in the type.

Mesonotum brown, without distinct markings; pseudosutural foveæ elongate, shiny brown. Pleura brown, sparsely gray pruinose. Halteres obscure yellow, knobs brown. Legs with the coxæ, trochanters and femora light brown; tarsi dark brown. Wings pale gray, unmarked; stigma lacking; veins pale brown. Venation: *2nd Anal* vein very strongly bisinuous.

Abdominal tergites dark brown; sternites slightly paler. Male hypopygium with the pleurites moderately stout; two pleural appendages; outer appendage subclavate, the apex blackened; inner appendage a pale flattened blade, the outer angle of which is recurved into an elongate acute point. Gonapophyses appearing as two slender curved horns, contiguous basally, diverging apically, the tips heavily blackened.

Habitat: Japan. Holotype, ♂, Nakano, May 27, 1920 (H. Machida).

Ormosia Rondani.

Ormosia nantaisana sp. n.

General coloration light gray; mesonotal praescutum with a median brown stripe; halteres golden-yellow; wings brownish gray, stigma and wing-tip darkened; cell *1st* M_2 closed, *m* short, Anal veins convergent; male hypopygium with the inner pleural appendage stout, subclavate, the apex set with microscopic black points.

Male—Length, 6 mm.; wing, 7.3 mm.

Rostrum and palpi dark brown. Antennæ with the scapal segments dark brown, the remainder broken. Head light gray, the vertex provided with numerous setæ, those of the disk yellow, the lateral bristles longer, dark brown.

Pronotum dark gray, provided with very long and conspicuous yellow setæ. Mesonotal praescutum light gray with a broad, indistinct, brown median stripe; lateral stripes indistinct; pseudosutural foveæ conspicuous, elongate, black; remainder of mesonotum gray pruinose. Pleura clear light gray, provided with groups of long yellow setæ on the mesepisternum and on the mesosternum. Halteres golden-yellow. Legs with the coxæ dark, sparsely pruinose, provided with conspicuous yellow setæ; trochanters dull yellow; remainder of the legs broken. Wings with a brownish gray tinge; stigma darker brown; wing-tip and the cord narrowly margined with brown; veins dark brown, *Sc* yellow. Venation: Sc_1 longer than *Rs;* R_{2+3} a little longer than the basal deflection of Cu_1; *r* on R_2 shortly beyond its origin; cell *1st* M_2 closed; *m* short, between one-third and one-fourth the outer deflection of M_3; basal deflection of Cu_1 slightly sinuous, beyond the fork of *M;* Anal veins strongly convergent.

Abdomen dark brown with conspicuous yellow setæ. Male hypopygium stout; two pleural appendages, inner appendage subclavate, the tip truncated, densely set with microscopic blackened points; outer appendage a slender flattened yellow blade, the apex subacute.

Habitat: Japan. Holotype, ♂, Nantaisan, August 16, 1909. Type in the Collection of the Paris Museum.

Ormosia takeuchii sp. n.

Related to *O. takahashii;* general coloration pale brownish testaceous; thoracic pleura and abdomen darker; wings pale gray; cell *1st* M_2 open by the atrophy of the outer deflection of M_3; Anal veins convergent; male hypopygium with the outer gonapophyses simple.

Male—Length about 4 mm.; wing, 4.3 mm. *Female*—Length about 3.8 mm.; wing, 4.4 mm.

Rostrum and palpi dark brown. Antennæ short in both sexes, pale brownish testaceous; flagellar segments with a conspicuous pale pubescence. Head pale with abundant yellow setæ.

Mesonotal praescutum pale brownish testaceous, unmarked with darker, the interspaces with conspicuous erect yellow setæ, lateral margins paler; remainder of the mesonotum brownish testaceous.

Pleura brown, very sparsely pruinose. Halteres pale yellow. Legs with the coxæ and trochanters obscure yellow; femora pale brown with yellow appressed setæ; tarsi brown. Wings pale gray, the stigma brown; veins pale brown; cells with an abundant pubescence. Venation: Cell *1st* M_2 open by the atrophy of the outer deflection of M_3; Anal veins convergent, the outer half of the *2nd Anal* vein bent towards the *1st Anal*.

Abdomen dark brown, the genital segment brighter; valves of the ovipositor horn-color. Male hypopygium very similar to that of *O. takahashii*, but the outer gonapophyses simple, conical, there being only six points surrounding the genital field.

Habitat: Japan. Holotype, ♂, Gifu, October 1, 1920 (K. Takeuchi). Allotopotype, ♀, October 10, 1920.

This interesting species is named in honor of its collector, Mr. K. Takeuchi, to whom I am indebted for much valuable material.

Gonomyia Meigen.

Gonomyia (Ptilostena) teranishii sp. n.

General coloration light gray; mesonotal praescutum with two narrow brown lines; pleura yellow, the dorsal pleurites brown; legs yellow; wings yellowish gray, the costal region yellowish; brown spots at arculus; origin of *Rs;* along the cord; tips of the radial veins and near the tip of vein *2nd A;* Sc_1 about equal to R_{2+3}; R_3 strongly recurved at its tip; abdominal tergites dark brown, the caudal margins of the segments very narrowly grayish.

Female—Length, 7.2 mm.; wing, 6 mm.

Rostrum and palpi dark brown. Antennæ with the first scapal segment light gray pruinose; second segment light yellow; flagellum dark brown, the segments oval. Head brown, the front and anterior part of the vertex light gray pruinose.

Pronotum dark brown, obscure yellow laterally. Mesonotal praescutum dark brown, gray pruinose, on either side of the broad median gray line a narrow brown line extending to the suture; humeral angles and lateral margins obscure yellow; scutum light gray, the centers of the lobes brown; scutellum and postnotum dark, gray pruinose. Pleura light yellow, the dorsal half dark brown, deepest anteriorly. Halteres obscure yellow, the knobs dark brown. Legs with the coxæ and trochanters light yellow; remainder of the legs yellow, the terminal tarsal segments brown. Wings yellowish gray, the costal and subcostal cells clearer yellow; brown spots at the arculus; stigma; along the cord; basal deflection of Cu_1; tips of veins R_2, R_3 and near the tip of the *2nd Anal* vein; extreme wing-tip cream-color, preceded by a faint brown suffusion; veins brown, *C* and *Sc* more yellow. Venation: Sc_1 extending to just beyond the origin of *Rs*, Sc_2 far from the tip of Sc_1, the latter alone about equal to R_{2+3}; *Rs* very strongly angulated

and slightly spurred at origin; R_{2+3} gently arcuated; R_2 short, straight, subperpendicular, nearly its own length beyond the end of R_1; R_3 curved strongly cephalad before its tip; inner ends of cells R_3, R_5 and *1st* M_2 in alignment; petiole of cell *2nd* M_2 a little shorter than R_{2+3}; basal deflection of Cu_1 far before the fork of M, about one and one-half times its length before the fork of M.

Abdominal tergites dark brown, the caudal margins very narrowly grayish; genital segment obscure brownish yellow; basal sternite yellow; intermediate sternites black, variegated with black, this coloration probably due to eggs beneath the surface; caudal margins of the segments narrowly yellowish.

Habitat: Japan. Holotype, ♀, Koiwai Farm, near Morioka, August 17, 1920 (C. Teranishi).

This handsome crane-fly is named for its collector.

Trentepohlia Bigot.

Trentepohlia (**Trentepohlia**) **septemtrionalis** sp. n.

General coloration brownish yellow; mesonotal praescutum with an indistinct brown stripe; femora yellow, the tips dark brown; tibiæ yellowish white, the bases and tips blackened; wings yellowish gray, stigma and the wing-axil darkened; *Rs* about two-thirds the deflection of R_{4+5}; petiole of cell R_5 short, about equal to *Rs*.

Female—Length, 8.4 mm.; wing, 6.5 mm.

Rostrum, maxillary and labial palpi dark brown. Antennæ dark brown, the second scapal segment paler, obscure yellow. Head dark brown, sparsely grayish.

Pronotum dark brown. Mesonotum obscure brownish yellow, the praescutum with an indistinct darker brown median line; scutal lobes darkened; postnotum testaceous. Pleura yellowish testaceous, sparsely dusted with yellowish pollen. Halteres pale. Legs with the coxæ concolorous with pleura; trochanters testaceous; femora yellow, the tips broadly but gradually dark brown; tibiæ yellowish white, the bases and tips narrowly darkened; metatarsi pale yellow; terminal tarsal segments brown. Wings yellowish gray; a small brown stigmal spot at *r*; *Cu* and branches narrowly seamed with brown; a conspicuous brown cloud in the anal angle of the wing; veins pale brown, *C*, *Sc* and *R* pale yellow. Venation: *R* straight, about two-thirds the deflection of R_{4+5}; basal section of R_{2+3} about one-half longer than the second section; petiole of cell R_5 about as long as *Rs* or the basal deflection of Cu_1, the latter immediately before the fork of *M*; fusion of Cu_1 and *1st A* about equal to the basal deflection of R_{4+5}.

Abdomen light brown, more yellowish basally. Ovipositor horn-colored.

Habitat: Japan. Holotype, ♀, Nakano, June 2, 1920 (H. Machida).

Trentepohlia septemtrionalis is the most northerly species of the genus yet discovered. Its closest relative is *T. nigro-apicalis* (Brunetti) of British India, which differs in the size, body-coloration and, especially, the coloration and venation of the wings.

Limnophila Macquart.

Limnophila (Phylidorea) melanommata sp. n.

General coloration shiny reddish yellow; antennæ with the basal segment dark brown, the remainder yellow; mesonotal praescutum with a narrow, dark brown median line that is narrowed behind; legs brownish yellow; wings light yellow, the wing-tip narrowly darkened; cord and inner end of cell *1st* M_2 narrowly darkened; *r* at the tip of R_1; cell M_1 present.

Female—Length, 9 mm.; wing, 8.2 mm.

Rostrum and palpi dark brown. Antennæ with the first scapal segment dark brown; remainder of the antennæ conspicuously and abruptly light yellow. Head dark brown, conspicuously silvery pruinose.

Pronotum obscure yellow, dark brown medially. Mesonotal praescutum shiny reddish yellow, with a narrow, dark brown median stripe, broadest in front, gradually narrowed behind, becoming obsolete before the suture; remainder of the mesonotum obscure yellow. Pleura reddish yellow. Halteres yellow, the knobs faintly darkened. Legs with the coxæ and trochanters yellow; femora obscure yellow, the tips very narrowly and indistinctly darkened; tibiæ obscure brownish yellow; tarsi darkening into brown. Wings with a uniform light yellow tinge; wing-tip narrowly margined with dark brown, this color extending from cell *2nd* R_1 to cell R_5, and thence more narrowly and less distinctly to cell M_3; narrow and indistinct brown seams at the origin of *Rs;* along cord and outer end of cell *1st* M_2; forks of R_{2+3} and M_{1+2}; stigma appearing as a narrow seam along *r* and the tip of R_1; veins yellow, darkened in the infuscated areas. Venation: *Sc* long, Sc_2 extending to about opposite one-half to two-thirds R_{2+3}, Sc_2 much longer than Sc_1; *Rs* moderately long, nearly twice R_{2+3}, strongly angulated at origin; *r* at the tip of R_1; inner ends of cells R_3, R_5 and *1st* M_2 nearly in alignment; petiole of cell M_1 a little shorter than the cell; cell *1st* M_2 rectangular, widened distally; basal deflection of Cu_1 shortly beyond midlength of cell *1st* M_2.

Abdomen yellowish testaceous.

Habitat: Japan. Holotype, ♀, Koiwai Farm, near Morioka, September 4, 1920 (C. Teranishi).

Limnophila melanommata is a strikingly beautiful member of the *ferruginea* (*adusta*) group.

Rhaphidolabina Alexander.

Rhaphidolabina gibbera sp. n.

General coloration pale brownish yellow; antennal scape dark brown, flagellum brownish yellow; mesonotum exceedingly gibbous; mesonotal praescutum with a median brown line that splits at the suture into two parallel branches which continue to the abdomen; legs pale yellow; wings relatively broad, yellowish gray, sparsely marked with dark brown; cell *1st* M_2 open by the atrophy of *m*.

Male—Length about 5.5 mm.; wing, 6.9 mm. *Female*—Length about 5 mm.; wing, 6 mm.

Rostrum and palpi brownish black. Antennæ 15-segmented; scape brownish black, flagellum conspicuously light brownish yellow; basal flagellar segments short-cylindrical, the terminal segments more attenuated. Head dark brown, sparsely pruinose.

Pronotum brown, darker medially. Mesonotum exceedingly gibbous, pale brownish yellow, the insect appearing hump-backed; praescutum with a median brown line that divides at the suture, each branch continued to the abdomen, the pale area enclosed including the centers of the scutum, scutellum and postnotum. Pleura whitish testaceous. Halteres brownish testaceous, the knobs dark brown. Legs with the coxæ whitish testaceous, the fore coxæ a little darkened; remainder of the legs pale yellow, only the tarsal segments a little darkened. Wings relatively broad, with a yellowish gray tinge, sparsely variegated with dark brown spots, arranged as follows: At Sc_2; a large area at the origin of *Rs;* along the cord; outer deflection of R_2 and along R_{1+2}; tips of all the longitudinal veins at the wing-margin; forks of M_{1+2} and $M_{3+4}Cu_1$; stigma feebly indicated; veins pale yellow, darker brown in the infuscated areas. Venation: Sc_2 some distance before the origin of *Rs*, the distance about one-half longer than the basal deflection of Cu_1; *Rs* relatively long, strongly angulated at origin; R_{2+3+4} shorter than the basal deflection of Cu_1, a little longer than *r–m;* deflection of R_2 close to the tip of R_1; cell *1st* M_2 open by the atrophy of *m;* petiole of cell M_1 a little more than twice the length of the cell; petiole of cell M_3 a little shorter than the cell; basal deflection of Cu_1 at the fork of *M*.

Abdominal tergites brown, the basal segments paler; sternites pale brown. Ovipositor elongate, dark brown, the tips of the valves bright horn-yellow.

Habitat: Japan. Holotype, ♂, Gifu, October 10, 1920 (K. Takeuchi). Allotopotype, ♀, October 2, 1920.

Rhaphidolabina gibbera is to be referred to *Rhaphidolabina* although cell *1st* M_2 is open and there are other slight differences between this fly and the genotype, *R. flaveola* (Osten Sacken) of Northeastern North America.

Oropeza Needham.

Oropeza candidipes sp. n.

Antennæ pale basally, intermediate segments bicolorous, terminal segments dark; general coloration buffy gray, praescutum with three darker gray stripes; pleura testaceous gray, striped longitudinally with dark gray; legs yellow, tibiæ and tarsi snowy-white; wings yellowish; stigma conspicuous, dark brown; abdominal sternites testaceous yellow, each segment with a small, triangular median dark brown spot at the caudal margin.

Female—Length, 14–14.5 mm.; wing, 12–14 mm.

Frontal prolongation of head short, pale above, slightly darker laterally palpi with the basal two segments pale, the terminal segments dark brown. Antennæ very pale, almost white, terminal segments darker, the intermediate segments bicolorous, the base of each segment being darkened. Head gray, darker gray behind.

Mesonotal praescutum buffy gray, with three broad darker gray stripes, the intermediate stripe narrowly split by a pale line; scutal lobes dark, pale medially; scutellum pale testaceous, dark brown basally; postnotum buffy gray. Pleura testaceous gray, longitudinally striped with darker gray along the ventral margin of the mesepisternum; mesosternum dark gray; dorso-pleural membrane almost whitish. Halteres pale, the knobs dark brown. Legs with the coxæ testaceous, the fore coxæ darker; trochanters whitish; femora yellow; remainder of legs snowy-white. Wings with a strong yellowish tinge; stigma dark brown; veins dark brown, those in the costal region more yellowish. Venation: *Rs* pale, without macrotrichiæ, one-half longer than the deflection of R_{4+5}; cell *1st* M_2 long and narrow; basal deflection of M_{1+2} longer than *m;* petiole of cell M_1 about two-thirds as long as cell *1st* M_2.

Abdominal tergites dark brown, about the basal third or less of each segment paler; sternites one to six pale testaceous yellow, the posterior median area of each segment with a small dark brown triangle. Ovipositor with the slender tergal valves dark brown; sternal valves flattened, pale.

Habitat: Japan. Holotype, ♀, Tamagawa, Saitama-Ken, August 30, 1920 (H. Machida). Paratype, ♀, Ikaho, Gumma-Ken, July 7, 1920 (K. Tanaka).

Tipula Linnaeus.

Tipula shomio sp. n.

Head dark gray; antennæ of male moderately elongate, indistinctly bicolorous; thorax gray, the praescutal stripes and scutal lobes shiny black; fore femora black, except the basal fourth, hind femora yellow with the apical fourth black; wings pale yellowish, the base and subcostal cell brighter yellow; disk variegated with brown and gray; abdomen yellow, with a subterminal brownish black ring; male hypopygium large, the ninth tergite produced into a hood-like median lobe; ninth pleurite complete.

Male—Length, 13 mm.; wing, 16 mm.

Frontal prolongation of the head dark brown above, paler laterally, black ventrally; palpi dark brown. Antennæ of the male moderately elongated, if bent backward extending a little beyond the wing-root; scape and basal two segments of the flagellum reddish yellow; remaining flagellar segments brown, the basal enlargement of each segment darker to give to the flagellum an indistinctly bicolorous appearance; terminal segments uniformly dark brown. Head dark gray pruinose.

Pronotum dark gray. Mesonotum with the praescutal stripes and scutal lobes shiny black, the former confluent or nearly so; median area of the scutum, scutellum and postnotum dark gray pruinose. Pleura dark, gray pruinose, an indistinct longitudinal stripe paler gray. Halteres obscure yellow, the knobs dark brown. Legs with the coxæ dark brown, gray pruinose, the tips of the posterior coxæ pale; trochanters obscure yellow; fore femora black with about the basal fourth abruptly brownish yellow; middle femora with the apical third black; hind femora with a little more than the apical fourth black; tibiæ obscure brownish yellow, the apical half brown; tarsi brownish black. Wings pale yellowish subhyaline, the wing-base and subcostal cell conspicuously light yellow; costal cell dark brown, pale at the base and apex; stigma dark brown, continued as a slightly paler brown seam along the cord to the posterior margin; wing-tip faintly darkened, this including the outer halves of cells R_2, R_3 and R_5, and as a very narrow seam around the wing-tip to Cu_1; a faint brown seam at the origin of *Rs;* brown seams along *Cu* and its branches and vein *2nd A;* grayish brown clouds in the ends of the Anal cells and as a faint cloud across the basal cells, beginning at the origin of *Rs;* the subhyaline color beyond the cord appears as a broad band in the basal half of cells R_2, R_3, R_5 and all of cell *1st* M_2; very narrow brown seams along the veins beyond the cord; veins dark brown, yellow in the yellowish areas. Venation: *r* joining R_{2+3} at its fork; R_2 oblique; *Rs* longer than R_3; cell *1st* M_2 small, pentagonal, about as long as cell M_1.

Abdomen obscure yellow, the tergites with three very indistinct capillary dark brown lines; a subterminal dark brownish black ring occupying segments six to eight, these segments broadly margined with obscure yellow; hypopygium yellowish brown. Male hypopygium large. Ninth tergite extensive, the median area produced caudad into a blunt black median lobe; viewed from beneath this lobe is seen to be hollowed out into a hood-shaped structure; dorsal-median area of the tergite sunken. Ninth pleurite complete, large; outer pleural appendage flattened, angularly bent, provided with a fringe of long yellow bristles; inner pleural appendage flattened, heavily chitinized; from the inner margin of the pleurite juts a small flattened blade, with a powerful chitinized spine along the margin. Ninth sternite feebly notched. Eighth sternite broad, the caudal margin broadly and very shallowly notched, the lateral angles with a sparse fringe of long, pale bristles.

Habitat: Japan. Holotype, ♂, Koiwai Farm, near Morioka, September 8, 1920 (C. Teranishi).

Tipula flavocostalis sp. n.

General coloration of the head and thorax gray, mesonotal praescutum trivittate with dark brown; halteres and legs yellow; wings subhyaline, wing-base and costal region conspicuously light yellow; stigma brown; sparse gray clouds on the wing; tip of R_2 atrophied; abdomen yellow, tergites trivittate with dark brown; a subterminal brown ring; male hypopygium cylindrical, tilted at an angle to the remainder of the abdomen; ninth tergite tridentate, the median blade very compressed.

Male—Length about 11 mm.; wing, 12.4 mm. *Female*—Length, 13–15 mm.; wing, 13–14.5 mm.

Frontal prolongation of the head dark brown above and beneath, brownish yellow laterally; palpi dark brown, terminal segment elongate. Antennæ of moderate length; scapal segments obscure yellow, the basal segment darkened basally; first flagellar segment brownish yellow; remaining flagellar segments dark brown, covered with a dense white pubescence; basal enlargement of each segment relatively small; in the female, the antennæ are more uniformly yellowish. Head light gray.

Pronotum obscure gray, indistinctly trinotate with brown. Mesonotal praescutum light gray with three indistinct dull brownish gray stripes, the intermediate stripe conspicuously margined with darker brown and split by a capillary dark brown line to appear trilineate cuneiform; remainder of mesonotum light gray, the centers of the scutal lobes darkened. Pleura uniformly gray. Halteres pale, the knobs yellow. Legs with the fore coxæ dark gray, the other coxæ obscure yellow, darkened basally, less extensive on the hind legs; trochanters and femora yellow; tibiæ and tarsi brownish yellow, the terminal tarsal segments passing into dark brown. Wings subhyaline, the base, costal and subcostal cells yellowish; stigma dark brown; vein *Cu* and branches seamed with dark brown; very pale gray clouds in the medial and anal cells; wing-tip slightly darkened, occupying the apices of cells R_2, R_3 and R_5; the subhyaline band beyond the stigma is broad and conspicuous; veins dark brown, *C*, *Sc* and *R* conspicuously light yellow. Venation: *Rs* long, a little shorter than R_3, about one-half longer than R_{2+3}, the extreme base indistinct; tip of R_2 beyond *r* atrophied in the male, in the female only the distal half of the outer section atrophied; cell *1st* M_2 relatively small, pentagonal; second section of M_{1+2} about twice the first section; *m* about one-third the outer deflection of M_{3+4}; petiole of cell M_1 about equal to cell *1st* M_2; *m-cu* distinct.

Abdomen dull yellow, the tergites narrowly trivittate with dark brown; a brown subterminal ring occupying segments six to eight, with the exception of the apex of the eighth sternite; hypopygium brownish yellow. In the female the abdomen is yellow, the tergites trilineate with dark brown, the fifth to seventh segments dark brown. Ovipositor chitinized, acicular. Male hypopygium cylindrical, tilted at an angle to the remainder of the abdomen, as in the *unca* (*hebes*) group, to which, however, the species does not appear to belong. Ninth tergite extensive, the caudal margin tridentate, the lateral lobes heavily

chitinized, the apices truncated and directed slightly proximad; median lobe a highly compressed blade; viewed from above appearing as an acute edge that is a little shorter than the lateral lobes; the notches between the lateral and median lobes are subcircular. Ninth pleurite complete; outer pleural appendage very short and stout; inner pleural appendage relatively small, the interior ends produced into curved, blackened hooks, the caudal angles produced caudad and slightly ventrad into slightly expanded blades. Ninth sternite extensive. Eighth sternite with the broad median lobe rounded, provided with a fringe of long setæ.

Habitat: Japan. Holotype, ♂, Tamagawa, Saitama, September 25, 1920 (H. Machida). Allotopotype, ♀, September 26, 1920. Paratypes, ♀, Gifu, October 1, 1920 (K. Takeuchi); ♀, October 10, 1920.

Tipula taikun sp. n.

General coloration gray; mesonotal praescutum with a narrow, brown median line; thoracic interspaces with small brown punctures; antennæ of the male moderately elongated; intermediate flagellar segments indistinctly bicolorous, the base of each segment yellowish; femora brownish yellow with a narrow subterminal brown ring; wings faintly brownish, the base yellow; costal and subcostal cells dark brown; subhyaline areas before and beyond the stigma; cell *1st* M_2 small, pentagonal; abdomen yellow, narrowly trivittate with dark brown; a brown subterminal ring; male hypopygium with the ninth tergite having a small median notch.

Male—Length, 11.5 mm.; wing, 13 mm.

Frontal prolongation of the head dark brown; palpi dark brown, the basal segment a little brighter. Antennæ of the male rather elongate, if bent backward extending about to the base of the abdomen; scape and first flagellar segment yellow; remainder of the antennæ dark brown, the basal half of the knobs of the intermediate segments yellow, producing an indistinct bicolorous appearance; terminal flagellar segments uniformly dark brown. Head gray.

Pronotum buffy, with a dark brown median mark. Mesonotal praescutum brownish gray with three nearly concolorous stripes; intermediate stripe narrowly margined for most of its length with dark brown, split medially by a narrow dark brown line; thoracic interspaces with brown setigerous punctures; remainder of the mesonotum brown, sparsely pruinose, split by a slightly interrupted capillary brown line. Pleura light gray pruinose, the dorso-pleural areas more brownish. Halteres light brown. Legs with the coxæ and trochanters obscure yellow; femora brownish yellow with a very narrow and indistinct dark brown subterminal ring; tibiæ brownish yellow, passing into dark brown at the tip; tarsi dark brown. Wings with a faint brownish tinge, variegated with subhyaline areas; wing-base yellow; cells *C* and *Sc* dark brown; stigma dark brown; brown seams along *Cu* and its

branches, the *2nd Anal* vein and the wing-tip; the subhyaline areas appear before the stigma in cell *1st* R_1, as a broad seam beyond the stigma, occupying the bases of cells R_2 and R_3; a small area near the end of cell *M* adjoining vein *Cu;* a small blotch in the *1st Anal* cell near vein *2nd A;* veins dark brown. Venation: Sc_2 ending beyond two-thirds the length of *Rs;* tip of R_2 pale, subatrophied; cell *1st* M_2 small, pentagonal; first section of M_{1+2} about one-half the second section; *m* about two-fifths of the outer deflection of M_3; petiole of cell M_1 about one-half the cell and about equal to cell *1st* M_2; *m-cu* short.

Abdomen yellow, the tergites narrowly trivittate with dark brown; caudal lateral angles of tergites two to six paler brown; an indistinct dark brown subterminal ring, including segment seven, and the adjoining parts of tergites six and eight; hypopygium obscure yellow. Male hypopygium with the ninth tergite extensive, the dorsal surface densely covered with long yellow hairs, the caudal margin with a small circular median notch, the broad lateral lobes thus formed produced into short, blackened, lateral points, the caudal margin of the tergite narrowly chitinized. Ninth pleurite relatively small, complete; outer pleural appendage flattened, moderately broad, narrowed basally. Caudal margin of the eighth sternite with a broad median notch, the margins provided with tufts of long bristles.

Habitat: Japan. Holotype, ♂, Koiwai Farm, near Morioka, September 8, 1920 (C. Teranishi).

Tipula autumna sp. n.

Related to *T. pluriguttata* Alexander (Formosa); coloration of thorax, including the pleura, clear gray; femora unicolorous brownish yellow; male hypopygium with the caudal margin of the ninth tergite broadly notched, with a small median tooth in the notch.

Male—Length about 12 mm.; wing, 13 mm. *Female*—Length, 15–16 mm.; wing, 13.8–15 mm.

Frontal prolongation of the head yellowish brown, above dusted with gray; palpi dark brown. Antennæ of the male relatively short; scape and first flagellar segment obscure yellow; remainder of the flagellum indistinctly bicolorous, the basal enlargement of each segment dark brown, the remainder of the segment paler brown; terminal segments uniformly darkened; basal enlargement of each segment relatively conspicuous. Head gray; vertical tubercle between the eyes relatively prominent, indistinctly bifid.

Pronotum light yellowish gray. Mesonotal praescutum yellowish gray with three clear gray stripes, the intermediate stripe margined and split by a capillary brown line; lateral stripes faintly darkened; thoracic interspaces with brown setigerous punctures; humeral region and lateral margins of praescutum paler; scutum gray, each lobe with two small brown areas; remainder of mesonotum gray with a very indistinct median brown line. Pleura gray. Halteres pale yellow, the knobs a little darker. Legs with the coxæ pale, sparsely pruinose;

trochanters yellow; femora and tibiæ brownish yellow, the tips not darkened; tarsi brown. Wings with a faint yellowish gray tinge, the base, costal and subcostal cells brownish yellow; stigma relatively small; wing-tip in cells R_2, R_3, R_5, M_1, *2nd* M_2, M_4 and Cu_1 slightly darkened; *Cu* and branches indistinctly seamed with brown; small obliterative areas before and beyond the stigma and across cell *1st* M_2. Venation: Sc_2 extending to about opposite three-fourths the length of Rs, the latter relatively long and straight; tip of R_2 pale; cell R_2 relatively small; cell *1st* M_2 pentagonal; *m* about one-third the outer deflection of M_3; petiole of cell M_1 a little shorter than cell *1st* M_2; *m-cu* short.

Abdomen obscure yellow, the tergites trivittate with dark brown, the dorsal stripe interrupted, on each segment appearing as a roughly triangular mark that is narrowed behind, scarsely attaining the posterior margins of the segments; lateral stripes relatively narrow and indistinct; a narrow subterminal brown ring, most evident on segment eight; hypopygium reddish yellow. In the female, the dorsal abdominal stripe is broad, in some cases continuous, in others interrupted at the posterior margins of the segments. Male hypopygium relatively incrassated. Ninth tergite having the caudal margin with a conspicuous median notch as in the related *T. taikun* sp. n., but in the present species there is a small, acute tooth at the base of the notch; lateral lobes terminating in small, truncated, chitinized points. Ninth pleurite complete; outer pleural appendage broad, flattened; proximal face of pleurite near the ventral caudal angle produced into a small, digitiform lobe. Ninth sternite with a broad V-shaped median notch. Eighth sternite narrowed posteriorly, the caudal margin with a broad V-shaped notch, each side of which bears a flattened sheaf of long, reddish bristles, decussate across the median line.

Habitat: Japan. Holotype, ♂, Gifu, October 1, 1920 (K. Takeuchi). Allotopotype, ♀, October 19, 1920. Paratopotypes, 2 ♀'s, October 19, 1920; paratype, ♀, Shibuya, Tokio, September 29, 1920 (H. Machida).

Tipula subcunctans sp. n.

Allied to *T. cunctans* Say (Eastern North America); general coloration gray, praescutal stripes brown; tips of femora and tibiæ brownish black; abdomen brownish gray, the tergites with an indistinct, capillary, brown median line.

Female—Length about 20 mm.; wing, 18 mm.

Frontal prolongation of the head obscure yellowish laterally, broadly gray above; palpi dark brown. Antennæ with the first scapal segment dark brown; second segment obscure reddish brown; first flagellar segment brownish yellow; intermediate flagellar segments indistinctly bicolorous, the base of each segment darker than the remainder of the segment; terminal flagellar segments uniformly dark brown. Front surrounding the antennal bases ochreous; remainder of the head buffy gray with a conspicuous brownish black line.

Mesonotal praescutum gray with three rather indistinct brown stripes, the intermediate pair narrowly separated by a pale line; lateral stripes paler, narrowly margined with darker brown; scutal lobes gray with two brown marks; scutellum and postnotum light gray pruinose. Pleura gray, the dorso-pleural membranes brownish yellow. Halteres dark brown. Legs with the coxæ gray, concolorous with the pleura; trochanters brownish yellow; femora brownish yellow, the tips broadly brownish black, broadest on the fore legs, narrowest on the hind legs; tibiæ light brown, soon passing into dark brown; tarsi dark brown. Wings brownish gray, the costal margin darker brown, this including the costal and subcostal cells and the stigma; veins dark brown. Venation: Cell *1st* M_2 short, a little longer than the petiole of cell M_1.

Abdominal tergites brownish gray, the basal tergites clearer gray; a narrow, interrupted, capillary, dark brown, median stripe extending from tergite to caudad, becoming indistinct at about segment six; caudal and lateral margins of the tergites rather narrowly pale, ochreous. Ovipositor with the dorsal shield black; the valves castaneous.

Habitat: Japan. Holotype, ♀, Sapporo, October 3, 1920 (S. Kuwayama).

Tipula latemarginata sp. n.

General coloration gray; antennæ of male elongate, black; mesonotum gray, the praescutum with three dark gray stripes that are indistinctly margined with brown; femora yellow, the tips broadly dark brown; wings comparatively long and narrow, with a strong brownish yellow tinge; stigma and a faint seam along the cord darker brown; abdominal tergites gray with a broad brown sublateral stripe; lateral margins of the tergites broadly buffy yellow; male hypopygium with the tergites fused with the pleurites; tergal region with a short, broad median lobe.

Male—Length, 13.5 mm.; wing, 15.4 mm.

Frontal prolongation of the head gray; nasus very long and slender; palpi dark brown. Antennæ of the male somewhat elongated, if bent backward extending about to the base of the abdomen; basal segment of the scape gray pruinose; second scapal segment reddish brown; flagellum black, the intermediate and terminal segments rather deeply incised, the basal enlargements of each segment subglobular. Head gray with a capillary black median line.

Mesonotal praescutum gray with three darker gray stripes that are very indistinctly margined with brownish; a capillary dark brown median line; scutellum and postnotum clear gray. Pleura gray, the dorso-pleural membrane light yellow. Halteres brown, the base of the stem brighter, the knobs darker brown. Legs with the coxæ gray pruinose; trochanters obscure yellow; femora yellow, the tips broadly dark brown, broadest on the fore legs, somewhat narrower on the posterior femora; remainder of the legs brownish black. Wings comparatively long and narrow, with a strong brownish yellow tinge; wing-base and cell *Sc* more yellowish; stigma brown; narrow brown seams along the cord and

at the origin of *Rs;* veins dark brown. Venation: *Rs* about one-half longer than R_{2+3}; cell *1st* M_2 comparatively long and narrow; petiole of cell M_1 shorter than *m; m-cu* distinct.

Basal tergite gray; second tergite reddish on basal half, sparsely gray pruinose; remaining abdominal tergites with a broad dorso-median gray line that is narrowly interrupted at the posterior margins of the segments; a broad dark brown sublateral stripe; lateral margins of segments one to seven broadly buffy yellow; caudal margins of tergites very narrowly pale; sternites gray pruinose; hypopygium dark, the outer pleural appendage pale. Male hypopygium with the sclerites fused into a ring, the suture between the pleurite and sternite indicated. Region of the ninth tergite with a short, broad median lobe, the caudal margin narrowly blackened, truncate or feebly bilobed. Outer pleural appendage short and broad, covered with a mixed short and long pubescence. Ninth sternite with a deep and very narrow median notch, the tumid lobes slightly pointed outwardly. Eighth sternite unarmed.

Habitat: Japan. Holotype, ♂, Kairakuyen, Sapporo, May 27, 1916 (S. Kuwayama). Paratype, ♂, Fukagawa, Ishikara-Ken, August 30, 1916 (S. Kuwayama).

Tipula trifida sp. n.

Male—Length 13.5 mm.; wing, 15.6 mm.

Generally similar to *T. latemarginata*, from which it differs in the following regards.

The type is badly discolored by moisture and the coloration of the body can be discussed in general terms only. Antennæ of the male shorter, the flagellar segments not so distinctly binodose. Wings slightly broader, the cord not seamed with darker. Venation: R_{2+3} shorter, less than the ultimate section of R_2; cell *1st* M_2 shorter and broader. Abdominal tergites with the pale lateral margins narrower. Male hypopygium of the general type of *T. latemarginata*, the tergite being entirely fused with the pleurite; median lobe of the tergite subtended on either side by a more slender, pointed lobe that is a little longer than the truncate median lobe. Ninth sternite not tumid as in *T. latemarginata*. Eighth sternite narrowly margined with pale, unarmed.

Habitat: Japan. Holotype, ♂, Sapporo, May 17, 1919 (S. Kuwayama).

Tipula nikkoensis sp. n.

Closely related to *T. insulicola*, but much darker colored throughout.

Female—Length, 12 mm.; wing, 11 mm.

Closely related to *Tipula insulicola* Alexander (Japan).

Frontal prolongation of the head dark; palpi brownish testaceous, the terminal segment dark brown. Antennæ indistinctly bicolorous, the basal enlargement of each segment dark brown, the color continued onto the pedicel. Head pale brownish testaceous.

Thorax badly crushed, dark brown, praescutal stripes not apparent in the unique type. Pleura dark brown. Halteres pale yellow, the base of the knobs a little darkened. Legs with the femora brownish yellow, the tips dark brown; tibiæ and tarsi dark brown. Wings with a brownish yellow tinge, cells *C* and *Sc* more yellowish; stigma oval, dark brown; wing-tip in cells R_2 and R_3 indistinctly darkened; branches of *Cu*, the cord and most of the veins beyond the cord indistinctly seamed with brown; an obliterative area before and beyond the stigma; another obliterative area crossing cell *1st* M_2 from the end of cell *M* into the base of cell M_4; veins dark brown, more yellowish in the costal region. Venation: *Rs* short, arcuated; R_2 straight, the distal section in alignment with the basal section; cell *1st* M_2 irregularly pentagonal; *m* punctiform or nearly so; petiole of cell M_1 longer than cell *1st* M_2; *m-cu* obliterated by the long fusion of Cu_1 and M_{3+4}.

Abdominal tergites obscure yellow, conspicuously margined laterally and caudally with dark brown; sternites obscure yellow, the margins indistinctly darker.

Habitat: Japan. Holotype, ♀, Nikko, Tochigi-Ken, July 9, 1920 (K. Tanaka).

Tipula kuwayamai sp. n.

Allied to *T. serricauda* Alex.; antennæ of male moderately elongate, the intermediate flagellar segments bicolored; mesonotal praescutum with four gray stripes that are narrowly margined with dark brown; wings whitish subhyaline, variegated with light and dark brown; abdomen reddish brown, the terminal segments dark brown; male hypopygium with the ninth tergite a chitinized saucer; female ovipositor with the tergal valves serrated.

Male—Length, 16 mm.; wing, 18–20 mm. *Female*—Length, 29 mm.; wing, 25 mm.

Frontal prolongation of the head grayish pruinose; palpi dark brown. Antennæ of male moderately elongate, if bent backward extending about opposite or slightly beyond the wing-root; first flagellar segment yellowish orange, the base pruinose; second and third segments yellowish orange; fourth and fifth segments bicolorous, the basal enlargement black, the remainder of each segment brownish yellow; the succeeding segments gradually darken into uniform brown; flagellar segments rather deeply incised beneath. Head gray with a capillary dark brown median line; vertical tubercle with an impressed line.

Mesonotal praescutum clear gray, the interspaces behind more buff-brown; four clear gray praescutal stripes, the intermediate pair more brownish except at their anterior ends, these stripes widely separated behind by a median stripe of the ground color; praescutal stripes narrowly margined with dark brown; scutum clear gray, each lobe with two brown circles, the anterior one with a clear gray center, the posterior one with a darker gray center; scutellum and postnotum gray, the latter with a capillary dark brown line. Pleura dark gray; dorso-pleural membrane obscure yellow. Halteres testaceous, the base

of the knobs dark brown. Legs with the coxæ dark gray; trochanters yellowish; femora and tibiæ yellowish, broadly tipped with dark brown; tarsi dark brown. Wings whitish subhyaline, variegated with light and dark brown; base of the wing, costal and subcostal cells more yellowish; stigma dark brown, this marking extending onto the fork of *Rs;* the white areas appear as a zigzag crossband beyond the wing-base, extending from cell *R* to the posterior margin of the wing in cell *2nd A;* an oblique line in cell *M* near midlength of the cell; a conspicuous white band beyond the cord; cells R_1 and R_5 largely whitish subhyaline; veins dark brown. Venation: Tip of R_2 preserved.

Abdomen with the basal five segments light reddish brown, the first segment more grayish laterally; segments six to nine dark brown, appearing as a subterminal dark ring; hypopygium more or less pale apically. Male hypopygium as in *T. centralis* Lw. and allied forms; ninth tergite appearing as a heavily chitinized saucer, the posterior lateral angles jutting caudad and dorsad as subacute blades; from each of these blades a narrow, oblique black ridge extends proximad near the median line deflected towards the caudal margin of the sclerite and becoming obsolete; anterior margin of the saucer a high ridge with a low, obtuse elevation near each end.

Female larger and much heavier bodied than the male. Lateral margins of the tergites narrowly pale. Ovipositor of the *arctica* type, the five basal teeth subacute, the outer teeth fused into a sinuous blade.

Habitat: Japan. Holotype, ♂, Maruyama, Sapporo, June 1, 1919 (S. Kuwayama). Allotype, ♀, Sapporo, 1916. Paratype, ♂, Sapporo, 1916.

This interesting fly is named in honor of its discoverer.

Nephrotoma Meigen.

Nephrotoma stygia sp. n.

General coloration shiny black; vertical tubercle orange; pleura with a whitish yellow spot before the base of the halteres and on the dorsopleural membrane; halteres yellow; femora yellow with the tips blackened, broadest on the fore legs, narrowest on the posterior legs; wings hyaline, stigma dark brown, a narrow brown seam along the cord; abdomen entirely black.

Male—Length about 12 mm.; wing, 10.5 mm. *Female*—Length, 15 mm.; wing, 11.5 mm.

Frontal prolongation of the head shiny black; palpi black. Antennæ with the scapal segments reddish brown; first flagellar segment dark brown; remaining flagellar segments obscure brownish yellow, on the terminal segments passing into brown. In the female, the flagellar segments are uniformly brownish black. Head black, the vertical tubercle conspicuous, orange.

Pronotum black, the lateral margins of the scutellum yellow, confluent with the dorsal pleural spot. Mesonotum entirely shiny black.

Pleura black; a small whitish yellow spot immediately cephalad of the halteres; a second spot of the same color on the dorso-pleural membrane. Halteres with the stem pale brown, the knobs light yellow. Legs with the coxæ black; fore trochanters brown; middle and hind trochanters black; femora yellow, the tips broadly blackened, on the fore femora including the apical two-thirds; on the mid-femora, about the apical fifth; on the hind femora only the apical eighth, or thereabouts; tibiæ obscure brownish yellow, the tips blackened; tarsi black. Wings hyaline, the base and subcostal cell more yellowish; stigma dark brown, conspicuous, continued along the cord as a conspicuous seam to cell *1st* M_2; extreme tip of the wing darkened; veins black. Venation: *Rs* short, about one-half longer than the deflection of R_{4+5}; cell M_1 narrowly sessile.

Abdomen shiny black. In the female, the basal half of the abdominal segments are shiny black, the apical half deep velvety-black. Outer pleural appendage of the male hypopygium elongate, tapering to the narrow point. Ovipositor reddish horn-color.

Habitat: Japan. Holotype, ♂, Ikaho, Gumma-Ken, July 7, 1920 (K. Tanaka). Allotopotype, ♀. Paratype, ♀, Chujenji, Tochigi-Ken, July 9, 1920 (K. Tanaka); ♂, Nikko, Tochigi-Ken, July 9, 1920 (K. Tanaka).

Nephrotoma neopratensis sp. n.

General coloration black; antennal scape orange-yellow, flagellum dark brown; anterior part of vertex orange-yellow; a dark brown spot adjoining the inner margin of eye; general coloration of thorax dull black; femoral bases yellow; wings grayish yellow, the cord and wing-tip infuscated; cell M_1 broadly sessile; abdominal tergites brown, the lateral margins of the segments obscure yellow.

Female—Length about 17 mm.; wing, 15.4 mm.

Frontal prolongation of the head obscure brownish yellow, black above. Antennal scape orange-yellow; flagellum dark brown. Head orange-yellow, the occiput and posterior part of the vertex dark brown, this color extending cephalad onto the vertical tubercle; a conspicuous brown blotch on either side of the vertical tubercle adjoining the inner margin of the eye; a narrow pale ring surrounding the eyes.

Pronotum dark brownish black, the scutellum yellow. Mesonotal praescutum dull black, the interspaces between the praescutal stripes gray pruinose; extreme humeral regions narrowly and obscurely yellow; scutum and central lobe of scutellum dull black; lateral sclerites of scutellum obscure yellow; postnotum black. Surface of mesonotum in fresh specimens probably pruinose. Pleura almost entirely dark, very sparsely variegated with obscure yellow. Halteres yellow, the knobs a little darker. Legs with the coxæ concolorous with the ground-color of the pleura; trochanters obscure yellow; femora yellow basally, the tips broadly blackened, broadest on the fore legs where they include about the distal two-thirds, narrowest on the hind legs where about

the distal third is darkened; tibiæ and tarsi brownish black. Wings with a faint grayish yellow tinge, more saturated at the wing-base and in cell *Sc;* stigma oval, dark brown; distinct brownish gray seams along the cord; faint gray seams along the cubital and median veins; wing-tip broadly darkened, this including the outer ends of cells R_2, R_3, R_5, M_1, *2nd* M_2, M_4 and Cu_1. Venation: Cell M_1 very broadly sessile.

First abdominal tergite brown, light gray pruinose, the lateral margins broadly yellow; remaining abdominal tergites dark brown, only the anterior lateral margins obscure yellow; posterior segments uniformly dark brown; sternites brown, pale caudally. Ovipositor with the basal shields shiny black, the valves light horn-yellow.

Habitat: Japan. Holotype, ♀, Maruyama, Sapporo, May 26, 1916 (S. Kuwayama).

Nephrotoma neopratensis is allied to *N. pratensis* (L.) of Europe. It resembles *N. pullata* (Alex.) but has the dark coloration even more extensive and with the venational details distinct; R_{2+3} considerably longer than *Rs;* cell *1st* M_2 larger and with *m-cu* at the fork of *M*.

Nephrotoma microcera sp. n.

Antennæ short in both sexes; flagellar segments unicolorous; mesonotal praescutum with three shiny reddish stripes; a velvety black mark at the ends of the transverse suture; a capillary brown line on the scutellum and postnotum; legs pale brownish yellow, tarsi darker; veins yellow, costal region more saturated; stigma pale; abdomen yellow, tergites trilineate with black; sternites with a capillary black median line.

Male—Length, 13–13.5 mm.; wing, 12–12.5 mm. *Female*—Length, 19 mm.; wing, 14.5–15 mm.

Frontal prolongation of head pale yellow above, brownish laterally; palpi brown. Antennæ short, in the male, if bent backward, not attaining the wing-root; scapal segments pale yellow, flagellum passing into dark brown before the tip. Head pale testaceous yellow, shiny; occipital mark not distinct.

Pronotum pale yellow. Mesonotal praescutum yellow with three shiny reddish to reddish brown stripes that are sometimes only faintly indicated; scutal lobes reddish, the median area yellow; a semilunate velvety-black line at the ends of the suture above the wing-root; scutellum reddish yellow with a capillary dark brown median line; postnotum yellow, with a conspicuous elongate triangular dark brown mark, the point directed caudad and not attaining the posterior margin of the sclerite. Pleura yellow, indistinctly variegated with reddish. Halteres pale brown. Legs with the coxæ shiny yellow; trochanters yellow; remainder of the legs pale brownish yellow; tarsi darker. Wings with a yellowish tinge, more saturated in the costal region, this color continued to the wing-tip; extreme wing-apex very narrowly margined

with dark brown; stigma pale yellow; veins dark brown, more yellowish in the costal region. Venation: Cell M_1 very short petiolate to narrowly sessile.

Abdominal tergites dull yellow, trilineate with black, the median line broader, very narrowly interrupted at the posterior margins of the segments; lateral margins narrower, very indistinctly interrupted at about one-third the length of each segment; sternites yellow with a capillary black median line that is slightly interrupted. Male hypopygium having the ninth tergite with a very deep U-shaped median notch. Outer pleural appendage elongate, tapering to the slender apex. Ninth sternite deeply incised, each half tumid. Eighth sternite with the margin feebly notched, without lobes or conspicuous bristles, the basal half of the sternite dark brown.

Habitat: Japan. Holotype, ♂, Komaba, Tokio, June 6, 1920 (H. Machida). Allotopotype, ♀, May 29, 1920. Paratopotypes, 3 ♂'s, 2 ♀'s, May 29 to June 6, 1920. Paratypes, ♂, Maruyama, Sapporo, July 18, 1916 (S. Kuwayama); ♂, Sapporo, August 25, 1916 (S. Kuwayama).

Nephrotoma minuticornis sp. n.

Generally similar to *N. microcera*, differing as follows: Lateral regions of the frontal prolongation of the head not conspicuously darkened. Mesonotal praescutum with the stripes black, the median stripe split by a capillary reddish line; each scutal lobe with two confluent black marks; no dark mark at the ends of transverse suture; scutellum and postnotum without a dark median vitta. Legs with the tips of femora and tibiæ narrowly darkened. Wings with cell M_1 subsessile to very short-petiolate. Abdomen obscure yellow; tergites with three very narrow black lines, the dorsal stripe much narrower than in *N. microcera*. Tergites seven to nine dark brown, with the caudal margins yellow; sternites with the capillary dark line more interrupted; eighth sternite dark brown basally. Male hypopygium with the notch of the ninth tergite much broader U-shaped. Eighth sternite with a deep notch, the margins of which are clothed with long, conspicuous, yellow bristles that are contiguous or decussate across the median line of the body.

Habitat: Japan. Holotype, ♂, Sapporo, (S. Kuwayama).

THE SYSTEMATIC VALUE OF THE MALE GENITALIA OF DELPHACIDÆ (HOMOPTERA).

By Walter M. Giffard.

During the past three years the writer has had an exceptional opportunity to study the male pygofer and genital organs of large collections of Dephacidae, including many types and paratypes, representing most of the species described from North America and the West Indies. Because of their constancy and reliability as a specific character these organs (which of course include the aedeagus or penis) are unquestionably of first importance to the student in making correct determinations. The use of color as a specific character has led to synonomy on account of there sometimes being four color forms in a species, the sexes of both the brachypterous and macropterous forms being different. And among these forms there is often considerable color variation. This naturally results in much perplexity to the student of these insects.

There have been and there are still strong objections by some workers (perhaps rightfully so) to base generic determinations on any *one* constant character, these preferring to accept a natural assemblage of characters from which to found the genus. A close examination and study of the collections previously referred to revealed in each of the genera (taking the genotype itself or its congeneric representative as a guide) a marked similarity in the form and character of the male genitalia within each genus, so that each of the genera studied could in a very large measure be determined at a glance by the structure of the pygofers and of the exposed genital organs alone, without recourse to other external characters. Within certain genera, as they stand at present, two or more types of genitalia are present and the question arises if such sexual characters, found only in one sex, should be used to erect new genera. In such cases it is highly improbable that the genus is monophylogenetic. In the erection of genera the hind tibial spur or calcar has not been considered as much as it should have been, even by Kirkaldy, Muir and Crawford, who have used it for subfamily and tribal divisions. In discussing the Liburnia ("Delphax")

group, Kirkaldy[1] states "the characters which appear to me to be of generic value in this section, lie in the genitalia and the tibial spur, though I am not prepared, without the examination of a large series of European and American forms, to formulate genera based on them." Again referring to genitalia in general, Kirkaldy[2] further suggests "that the genitalia in the male are the final test of a species and even afford generic criteria."

Fieber[3] appears to have been the first to use characters found in the pygofer, anal segment and genital styles for specific purposes and most workers, with a few notable exceptions, have continued their use in certain groups of genera. Edwards[4] appears to have been the first to dissect and figure the aedeagus to distinguish certain allied species. Muir[5] in working out the Hawaiian Delphacidæ, placed greater weight upon the aedeagus and used the male genitalia not only for specific purposes, but also to rearrange the genera. He afterwards found other characters that confirmed his conclusions drawn from the genitalia alone.

In anticipation of using the genitalia in a similar manner Mr. Muir and the author are at present at work upon the North American and West Indian species. In the hopes of interesting students in these organs as characters of systematic importance, the following short description of the methods employed and the terminology decided upon, is presented. Morphologists may disagree with these terms and suggest using others that show the homology with other insects, but until we are sure what those homologies really are it is best to use purely descriptive names, most of which are already in use.

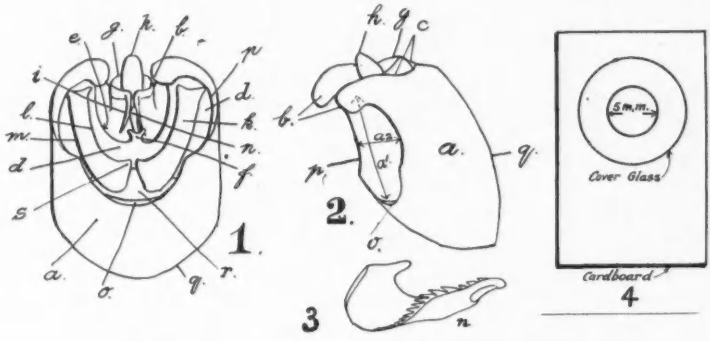
---

[1]Kirkaldy, Haw. Sug. Pl. Ass. Report 1907 Div. of Ent. Bull. III, p. 150.
[2]Op. cit. page 124.
[3]Fieber Verhandl. Zool. bot. Ges. XVI, 1866, p. 517-534, Pl. VIII.
[4]Edwards Hom. British Islands, 1896, pl. 6.
[5]Muir Proc. Haw. Ent. Soc. III, 3, 1916, pp. 221, pls. 2, 3, 4.

Nomenclature of Genitalia.

(See Figures 1, 2 and 3).

What is apparently the ninth abdominal segment in Delphacidæ is specialized into a more or less long, chitinous ring (***the pygofer*** (*a*)) without any clear trace of tergum, sternum or pleura. The posterior dorsal edge is more or less deeply emarginate (***anal emargination*** (*c*)) and more or less surrounds the ***anal segment*** (*g*); the corners of this emargination are more or less angular (***anal angle*** (*b*)) and in some species are considerably produced; the ***lateral margins*** (*p*) vary in shape, being straight and entire, produced or excavated; the ***ventral margin*** (*o*) also varies in the different species. The relative length and breadth of the opening (a_1, a_2) is also important. The tenth and eleventh abdominal segments form a small tube (***the anal segment*** (*g*)) which lies more or less surrounded by the ***anal emargination*** (*c*) ***of the pygofer.*** The anus opens on this latter segment and below or ventrad of the anus is the ***anal style*** (*h*); on the ventral surface of the anal segment are the processes of the anal segment (***anal processes*** (*i*)) generally in the form of a pair of spines. Looking into the opening of the pygofer one sees a more or less chitinous wall dividing it into an outer and inner chamber. This is the ***diaphragm*** (*d*) the ***dorsal margin*** (*e*) of which is generally V-shaped and often in the middle there is developed an ***armature*** (*f*); near the ***ventral***



Figs. 1 and 2.

a. pygofer; a^1, a^2, opening of pygofer (a^1 length, a^2 breadth).
b. anal angle of pygofer.
c. anal emargination of pygofer.
d. diaphragm.
e. margin of diaphragm.
f. armature of diaphragm.
g. anal segment.
h. anal style.
i. anal process of spine.
k. genital style.
l. inner margin of genital style.
m. outer margin of genital style.
n. aedeagus (or penis).
o. ventral margin of pygofer.
p. lateral margin of pygofer.
q. base of pygofer.
r. orifice of diaphragm.
s. basal angle of genital style.

Fig. 3.

n. aedeagus.

Fig. 4.

Details of card mount.

edge or margin (*o*) of the pygofer the diaphragm is pierced by an *orifice* (*r*), through which the genital styles pass. The length of the diaphragm is from the dorsal margin in the middle to the orifice. In the Delphacidæ there is always one pair of *genital styles* (*k*) which are of various size and shape; the terms *inner* (*l*) and *outer* (*m*) margins are of use in descriptive work, also the *basal angle* (*s*). The *aedaegus* (*n*) arises from the bottom of the inner chamber and when at rest its apex generally projects over the middle of the dorsal margin of the diaphragm, just above the armature. There is an internal structure connecting the anal segment to the base of the genital styles, which can be termed the connecting structure.

The Dissection and Treatment of the Pygofer and Genital Organs.

For ordinary purposes, when comparing the margins of the pygofer and exposed genital organs of a species under examination with any illustration or figure, the binocular microscope is much preferable to the hand lenses ordinarily in use and students should by all means use the former when possible. The size and opaqueness of these organs in very many of the species are such that in careful systematic work even the binocular, without an electric illuminator or condenser,* is insufficient to secure a proper and correct view of their structure. With an abundance of material to choose from, one might, on occasion, select an example which would result satisfactorily without the illuminator, but otherwise the student is quite apt to draw wrong conclusions.

The structures of the genital organs contained within the aperture of the pygofer are, as previously stated, of the greatest importance for correct determination of the species and these must therefore not only be viewed by the observer under the best of conditions, but on occasion the aedeagus, genital styles and anal tube must be dissected out. The aedeagus itself is so hidden behind the diaphragm of the pygofer that it is seldom visible, even with the strongest of illuminations and magnification. The anal tube, whilst visible, in a measure, with the hand lens or binocular, has in very many instances spines or processes of various lengths attached to its medio ventral surface, which are either quite invisible or are obscured by the genital styles. In many instances specimens, as ordinarily viewed, have their genital styles resting at a different angle than when they are normally at rest, which fact is quite sufficient to alter the outline and lead to error. This can easily be overcome if the styles are dissected out and a flat view taken.

The dissection of the genital organs is simple, if reasonable care is used. The method adopted by Mr. Muir and the author is to carefully sever the pygofer from the abdomen, transferring it to a 50% or 60% solution of Caustic Soda and boiling it over an alcohol flame in an

* The author has used with much success the B. & L. micr. lamp with aspheric condenser and transformer for 110 V. alternating current. The smaller and cheaper B. & L. illuminator and condenser has not been altogether satisfactory for this special work.

ordinary test tube for a few seconds only. The success of the method depends largely on the boiling process, for if it is boiled too long the clearness of structural detail is spoiled, whilst if it is not boiled enough, much fatty matter will remain attached to the organs to be observed, thereby causing some slight inconvenience in their further dissection and observation. It is, however, far better to underboil than otherwise. The student will soon learn to detect by the size, condition and appearance of the pygofer just what time is required in this boiling process. From the Caustic Soda the specimen is immediately transferred to water in order to wash and clear it. For this, it appears preferable to use a concave glass slide, so that the object may be kept under better control whilst under the binocular microscope. During this clearing process in water, the genital organs should be dissected out from the pygofer. This is done by means of fine needle points, with handles attached, holding the pygofer down with one needle whilst inserting the other through its anterior opening and pushing outwards the organs until all these are plainly visible. If it is intended to make a microscopic slide of the genitalia further manipulation and dissection under the binocular will be necessary in order to free the organs from the diaphragm or wall of the aperture of the pygofer, but for ordinary purposes of identification the pygofer together with the protruding organs can, without further process, be transferred with a very fine camel's hair brush or the point of a needle to the card point on which the insect specimen is mounted. Care must however be taken not to crush or smother the parts during manipulation and the mounting on the card point must also be carefully done, otherwise the organs will appear distorted and useless. Before mounting in balsam it is necessary to transfer the pygofer and genital organs into absolute alcohol in order to dehydrate and harden these. A few minutes only is required and the organs should then be cleared by transferring them from the alcohol to clove or cedar oil. In either one of these latter they may remain for a few hours, if necessary, but if speed is desired, four or five minutes is all that is required.

Some have objections to the microscopic slide process, as the slides have to be kept apart from the cabinet specimens; and again others claim that there is apt to be an absence of detail as shown by the "card point" system. To these may be suggested another and very acceptable method of permanently disposing of their dissections and at the same time keeping these attached to, or alongside, the insect specimen in their cabinets. This system has been called the Balsam card cell process,* and it has been used to an appreciable extent for the mounting of the genitalia of type specimens. For the purpose, rather stout Bristol board mounts of uniform size should be used (See Figure 4).

* Similar cells to these can be used without balsam for mounting delicate types, the insect being fastened with a small drop of clear gum to the bottom cover glass. Dr. David Sharp has types of small Staphalinidæ so mounted which can be viewed dorsally and ventrally under a fairly high power. The probability of damage or destruction of such specimens is greatly reduced by using this method.

A cell about 5 mm. in diameter must be smoothly punched towards one end and a 12 mm. circular or square cover glass be gummed or otherwise attached to the underside of the mount and allowed to dry (under cover) for several days before using. A stock of these may be prepared ready for use when necessary. Instead of entirely dissecting out the genital organs from the pygofer, as would be done for making a slide, manipulate and prepare the object as would be done for mounting on card point, taking care, however, that the dissection has later been transferred to alcohol and then into either Xylol or Clove oil before it is finally transferred to the Canada Balsam cell. The transfer from Clove oil or Xylol to the cell (in which a drop of Balsam has been placed) and the manipulation required to secure a proper lateral view of the margin of the pygofer, the armature if any, the anal tube and spines, the genital styles and aedeagus, is a delicate process, but fairly easy after a little experience. Before placing the final cover glass over the object it is well to wait a day or two and be sure that the object has not changed the desired position and that further manipulation is not required. Should a change be necessary, soften the Canada Balsam by passing the mount quickly, for a second or two, over the alcohol flame then using Xylol on needle points to alter the position of the objects. Once assured that the mount is satisfactory, another drop of Canada Balsam to take the final cover glass will end the process and give the student a perfect and permanent specimen of the genital organs. The pin of the insect mount can be run through the end of card cell and so allow the specimen and mount to be placed in the cabinet together. If the card cell sags, a small piece of cork can be glued to the underside of the card cell where the pin pierces it.

THE HAWTHORN BLOSSOM WEEVIL (ANTHONOMUS NEBULOSUS LEC.)*

WALTER H. WELLHOUSE.

One of the most interesting and injurious of the insects found on the hawthorns is this member of a very destructive genus of blossom weevils. Its mode of life resembles in a general way that of the Mexican cotton boll weevil, *Anthonomus grandis*, and is almost identical with that of the European apple blossom weevil, *A. pomorum* (see Theobald, 1909, p. 104-110).

The original description of *A. nebulosus* by Dr. Leconte may be found in the Proceedings of the American Philosophical Society 15:197, 1876, and a more complete description is given by Dietz in the Transactions of the American Entomological Society, 18:203, 1891. In the present account it is sufficient to say that *A. nebulosus* is a brown or grayish oval beetle, 3.75–4.25 mm. long, generally with a whitish V-shaped mark on the fore part of the elytra, with a long slender curved beak, and the front femur bearing two teeth on its apical portion, one a large and the other a small tooth.

It has been found in New York, New Jersey, Michigan, Indiana, Missouri, Arkansas and Louisiana, so it seems probable that it is present wherever its hosts are found East of the Rocky Mountains. Although Dietz considers this species to be more characteristic of the European fauna than of our own, no record can be found of its occurrence in Europe or elsewhere outside of our country.

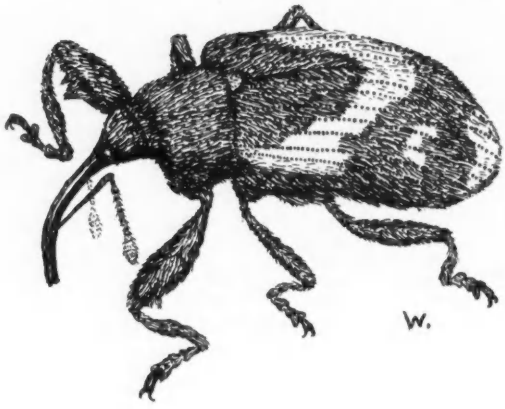
Its hosts include a number of the larger flowered species of hawthorns, such as *Crataegus punctata*, *C. brainerdi*, *C. pruinosa* and *C. mollis*. The smaller flowered species such as *C. oxyacantha* are not selected by the beetles for oviposition, probably because there is not space enough for the full development of the larva within the bud.

The injury caused by the hawthorn blossom weevil is most apparent while the trees are in full bloom. At that time infested blossoms are brown and remain closed. On badly infested trees fully 50 per cent of the blossoms may be in that condition and the trees present a scorched appearance. As

* Contribution from the Entomological Laboratory, Cornell University, Ithaca, N. Y.

the young fruit begins to set the infested blossoms commonly fall to the ground, but may sometimes be seen on the trees even after the beetles have emerged in June.

They come out of hibernation and appear on the branches of the hosts about mid-April, feeding ravenously on the buds which are showing green. It is not uncommon to see a beetle with feet braced and beak inserted up to the eyes in a bud while it hurriedly eats the tender leaves within. As soon as all the food within reach of the entrance hole is eaten, the beetle seeks another bud on the twig and repeats the process. The puncture in the bud is round, .3 mm. in diameter, and turns



dark as soon as the beak is withdrawn. The presence of the beetles may be detected by these dark round holes in the buds before the egg-laying period arrives. They continue to feed on the buds during suitable weather until the clusters have separated enough for oviposition in the blossoms.

During cool weather they remain inactive, generally in the axils of the twigs with heads down. A few observations on the relation of temperature to their activities were made, and these indicate that the beetles remain inactive while the temperature is below 50° F. The optimum temperature is 60° to 70° and when it is raised to 78°, they rush about like mad, attempting to oviposit in every bud. Under most conditions they seem reluctant to fly, but when placed on distasteful food

they fly away. They continue their activities on cloudy or rainy days and at night if the temperature is sufficiently high.

The period between the opening of the blossom clusters and the opening of the blossoms themselves is the time of oviposition, and the length of this period probably influences the amount of injury to a considerable extent. If it is prolonged by cool, cloudy weather, then eggs may be placed in more blossoms before they open. The oviposition period comes about May 15 at Ithaca.

After selecting a suitable blossom bud the female makes a hole in the side of the calyx with her beak, then turning around she thrusts the egg into the hole with her ovipositor and moves to another bud to repeat the process. A clear liquid fills the hole where the egg is thrust in, which soon hardens and seals the opening completely. The act of oviposition requires about 10 minutes when the temperature is 68° or 70°, but requires an hour at 54°.

The egg is pearly white, .6 mm. long, .36 mm. wide, elliptical generally the same size at both ends, but when tucked in tightly between the anthers it may be narrower at one end to conform to the space it fills. It is almost the same size and color as the anthers and difficult to distinguish from them. The corium is smooth, unsculptured, delicate, drying and collapsing when exposed to the air for one hour.

After about a week the young white curved legless larva is found within the bud. It feeds upon the anthers and as it grows consumes all the internal parts of the flower, but leaves intact the wall of the receptacle and the closed petals which form the roof of its house. The petals become stiff, as if they were starched, and do not shrink away as they turn brown. After feeding a couple weeks, the larva is dirty white, 6 to 8 mm. long, legless, has a small brown head and lies in a curved position. At about this time it moults and changes to a white free pupa 6 mm. long, with a dark caudal spine, 2 dark prominent spines on the apex of the head and several smaller spines farther back on the head. After pupating during a week or a little longer, the beetle makes a hole in the top or side of its house with the beak and emerges.

It begins to feed a few minutes after emergence, choosing for its food the first young thorn or fruit in its pathway as it wanders along the branch. The thorns of the current season's

growth seem to be a very attractive food. A hole is drilled near the base of the thorn and the beetle will spend hours with the beak inserted in the hole clear up to the eyes, prying and straining to enlarge the cavity within the thorn. The round hole at the base of a thorn does not heal during the season's growth and the presence of such holes will indicate at any time of the year the presence of the blossom weevils. The beetles also attack the fruit and make several round holes in a single fruit before seeking another. The holes become brown almost immediately. I have never found the beetles eating leaves or tender twigs, but they sometimes feed on the succulent globular leaf galls of cecidomyiid larvæ. They will puncture and feed on young apples in the cages when fresh haws are not to be had, but I have found none feeding on apples in the field.

After feeding for a week or ten days the beetles may be found in copulation on the branches, and a week or so later, as warm July weather comes, they disappear from the trees. Those kept in breeding cages remained hidden in fallen curled leaves and hollow twigs on the ground all summer and winter without feeding until the next spring. A search for their hiding places in the field revealed a score of the beetles enclosed in curled dried leaves on the ground beneath their host trees.

The life cycle may be summarized as follows: The immature stages (egg, larva and pupa) are completed within the closed blossom in from 27 to 35 days and the remainder of the year is passed in the adult stage. The adults feed on thorns and fruit for two or three weeks after emerging from the blossoms, then remain quiescent among fallen leaves on the ground until the next spring, when they feed for about a month on the buds before ovipositing. Soon after oviposition the beetles die. In New York the eggs are laid about mid-May and the beetles emerge from the blossoms in June. Pierce says the beetles emerge in late March and early in April in Louisiana. The time of their development in different latitudes is dependent on the opening of the hawthorn blossoms in those latitudes.

A number of natural enemies of the blossom weevil have been observed. Various birds and especially sparrows pick open the brown blossoms to eat the larvæ and pupæ. Pierce found them to be parasitized by *Catolaccus hunteri* and *Sigalphus* sp. (U. S. Bur. Ent. Bull. 100, p. 77). The writer has bred another chalcid, *Habrocytus piercei* Cwfd. from the larva of the weevil, the adult parasites emerging June 16th and 17th.

SOME NEGLECTED SETÆ OF LEPIDOPTEROUS LARVÆ.

By HARRISON GARMAN.

A study of the corn-ear worm larva with reference to its external structure* has revealed series of microscopic setæ, some of which appear to have been overlooked by other writers when dealing with the Noctuidæ and are thus not recognized in the systems employed, though they are as constant in every way as the larger setæ to which numbers, or Greek letters, have been assigned. As opportunity arose the author has examined larvæ of other families of moths and finds the same setæ present, though showing some variations with family, in their numbers, in position on the body, and in their relation to each other and to certain of the large setæ. As examples of these variations I am presenting figures made from greatly enlarged photographs of the skins of one of the Cossidæ, *Prionoxystus robiniæ*, the well known Carpenter worm of black locust trees, and of *Tholeria reversalis*, one of the Pyralidæ.

The body of the carpenter worm when about half grown bears round brownish tubercles upon which the setæ arise, the pigment of the tubercles serving as a guide in locating the setæ and enabling one to find with no special difficulty even the smallest of them. This larva bears six large setæ on each side of its neck plate, and one microscopic seta at the posterior edge of each half, the latter being the homolog of the one noted on the neck plate of Chloridea. The neck plate bears also on each side three sense pores, the lateral one minute, and a gland outlet outside and a trifle posterior to seta IIa. A ventral microscopic seta is present on the prothorax anterior to the base of the jointed leg, and a second just in front of the base.

The mesothorax and metathorax are alike in the number and arrangement of setæ. A single microscopic seta is present at the anterior edge nearly in line with seta IIb of the neck plate. Exterior to these setæ, in line with the ventral sense pore of the neck plate, is on both meso- and metathorax a pair of microscopic setæ; otherwise the microscopic setæ are like those of the prothorax. The fourth body somite (1st abdominal) bears a seta at its anterior edge, in line with the one on the thoracic somites, but lacks the lateral pair of microsetæ as does also the succeeding abdominal somites, but the microscopic seta IIIa appears before the spiracle as an independent seta. The more

* Bulletin No. 227, Kentucky Experiment Station.

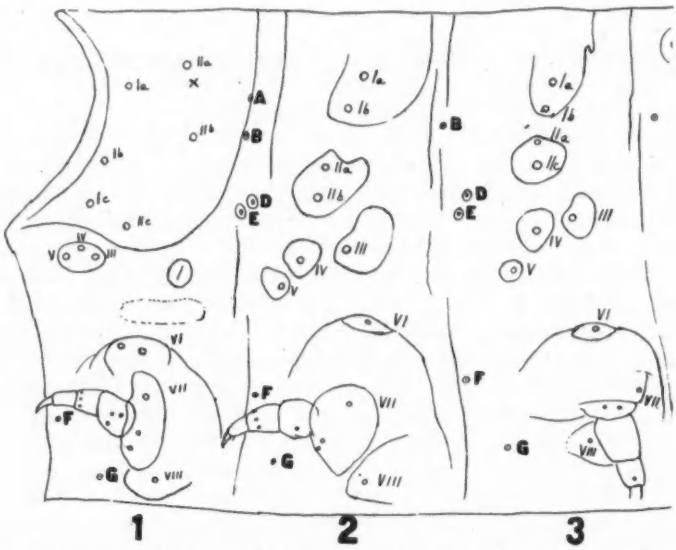


Fig. 1. Left side of larva of *Prionoxystus robiniæ*, showing the three thoracic somites. Sockets of large setæ (and IIIa) numbered by Dyar's system. Microscopic setæ indicated by letters. Gland of neck plate indicated by x.

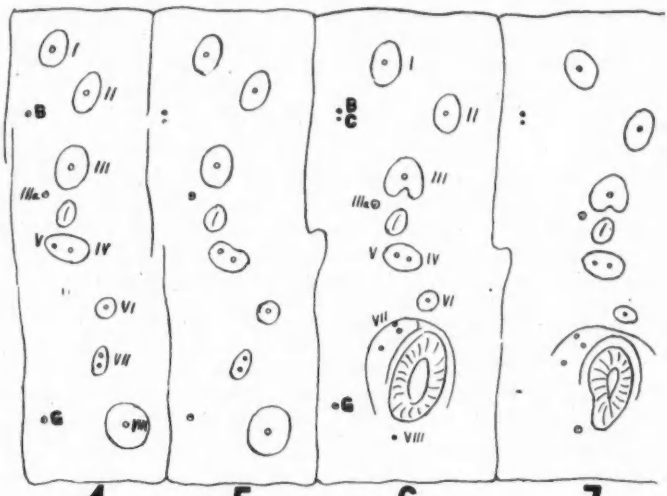


Fig. 2. Left side of larva of *Prionoxystus robiniæ*, showing body somites 4 to 7, inclusive (abdominal somites 1 to 4, inclusive). Letters and numbers as in Fig. 1.

dorsal of the two ventral microscopic setæ of the thorax disappears, and is lacking also on succeeding abdominal somites.

The fourth body somite (2nd abdominal) bears a pair of microscopic setæ in the dorsal series, the outermost vestigial; and on all following somites to and including the 12th body (9th abdominal) this pair is present, the two becoming somewhat widely separated on the 11th and 12th.

The larva of *Tholeria reversalis* has been taken in some numbers on several occasions from Laburnum in nurseries in Kentucky. It is a particularly fine larva for the study of setæ, because the bristles are borne on dense black, often angular, plates, and can be even more readily located than in the larva of *Prionoxystus robiniæ*. The same number (6) of macroscopic setæ is present on the neck plate, with three sense pores, as in Noctuidæ and Cossidæ. A microscopic seta is present at the posterior edge of the neck plate. The microscopic setæ of the meso- and metathorax are as in Prionoxystus, except that the pair is mounted on a pinaculum on each of these somites, the plates having apparently united. The dorsal series of microscopic setæ consists of a single seta near the anterior margin of somites 4 to 12 inclusive. The microscopic seta IIIa is in this larva associated on a hammer-shaped plate with the larger seta III, and is to be recognized on body somites 4 to 11 inclusive. The presence of IIIa with III on a pinaculum is a feature in which it agrees with Hepialus and certain Tortricids and differs from Prionoxystus.

A singular dermal gland with contorted chitinous efferent tubule opens on each side just posterior and a trifle ventral to the dorsal microscopic seta, on body somites 2 to 11 inclusive. Each efferent tube opens by a funnel-shaped enlargement in the cuticle. One of these glands and tubes opens also in the neck plate, and one in the base of each jointed leg. These are probably glands of the same nature as those described by E. Verson (See Packard's Text Book of Entomology) and said to give off oxalate of lime at an early stage, and later, uric acid. But it seems unlikely that special excretory organs are needed in this larva and not also in Noctuidæ. They have not at any rate been observed in Chloridea. In Prionoxystus there is a small aperture outside seta IIa of the neck plate, that probably represents these glands. It is liable to be mistaken for a fourth sense pore. The glands may produce some defensive excretion, but the efferent ducts are suggestive of the nephridia of Annelids, and it may prove that they are accessory renal organs as has been suggested. In the figures, the outlets of these glands are marked by an x.

The large setæ that have received numbers according to Dr. Dyar's system are indicated by these numbers in accompanying drawings, the homologies being determined by comparison of the photographs with figures published by Mr. Carl Heinrich* and made from larvæ of the same family in each case. In my own figures the microscopic setæ not represented by Mr. Heinrich are indicated by letters.

* Proc. U. S. Nat. Mus., Vol. 57, pp. 53-96, 1920.

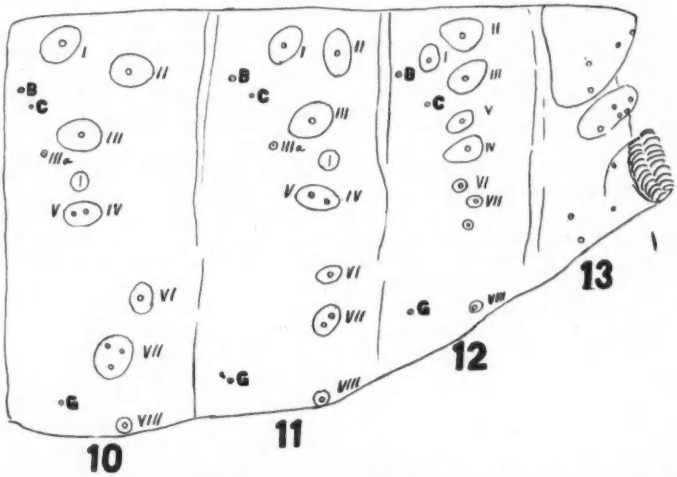


Fig. 3. Left side of larva of *Prionoxystus robiniæ*, showing body somites 10 to 13, inclusive. Letters and numbers as in Figs. 1 and 2.

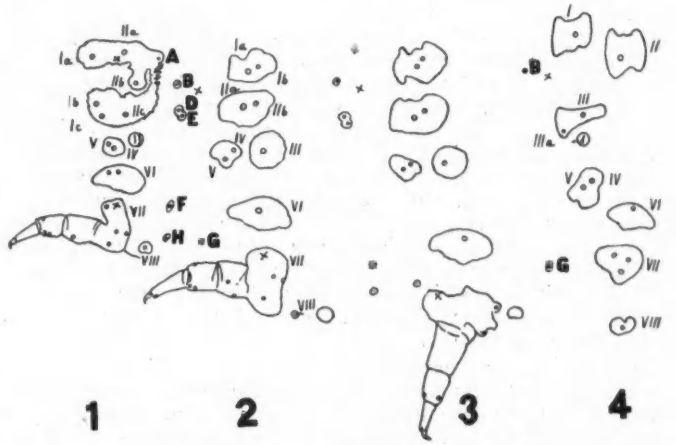


Fig. 4. Left side of larva of *Tholeria reversalis*, showing body somites 1 to 4, inclusive. Letters and numbers as in Figs. 1–3. Location of dermal glands marked by x.

It is evident from an examination of these larvæ that Dr. Dyar's numbers will some time require rearrangement so as to include in their appropriate places all of the setæ now known to be present on the bodies of lepidopterous larvæ.

The microscopic setæ must be considered in any complete system showing the chaetotaxy of our species. They are clearly a long-established feature of the structure of many families, and their vestigial character appears to denote some change in the integument of somites the nature of which we do not at present understand. Some or all of the setæ appear even among the confusing development of secondary setæ in such families as Arctiidæ and Notodontidæ. On the larva of

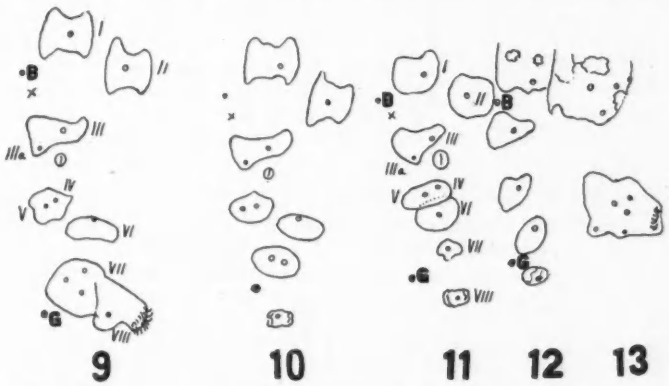


Fig. 5. Left side of larva of *Tholeria reversalis*, showing body somites 9 to 13, inclusive.

Acrolophus mortipenellus (Acrolophidæ) the paired setæ (D. and E. of my Figures) of the thorax are borne by a sclerite of some size, not different from those bearing the large setæ. The minute seta (A) of the neck plate is present in most of our families of moths. Seta IIIa is also generally present, though it has often been overlooked.* The others when sought out have proved not less constant, and once their location on the body is known, one can on a large number of our genera count with certainty on finding them when this portion of the cuticle is brought under the microscope.

* It does not, however, always bear the same relation to III even in the same subfamily. Thus in *Tholeria reversalis* it is associated with III, but in *Desmia funeralis* it is independent.

STUDIES ON THE RESPIRATION OF INSECTS.

I. The Gases and Respiratory Proteins of Insect Blood.

Richard A. Muttkowski, Ph. D.

(Contribution from the Zoological Laboratory of the University of Idaho, Moscow, Idaho).

PAGE

1. Introductory....150
2. Oxygen and Respiratory Proteins in Insect Blood....151
3. Carbon Dioxide in Insect Blood....154
4. The Role of Insect Blood....155
5. Summary....156
6. Bibliography....156

I. Introductory.

The following paper aims to present certain phases of investigations on the respiration of insects. In a recent article (see Bull. Brooklyn Ent. Soc., 15, pp. 89-96, 131-140) I called attention to the fixation of oxygen by the blood of some aquatic insects. "In a few rare cases," it was stated (p. 94), "the carrier is colored. Thus, in some species of Chironomidæ, the pigment is hemoglobin, like that of Vertebrates, except that it is found in the plasma, not within the corpuscles. * * * The oxygen diffuses through the epidermis just as in the case of vertebrates, and is fixed by the hemoglobin or other carrier (perhaps hemocyanin?) in the blood. Just what this other carrier may be is not definitely ascertained. But by far the larger number of aquatic insects have no visible colored carrier or respiratory pigment. Thus, for example, Trichoptera larvæ, the larvæ of Simulium, of Culicidæ, and of most Chironomidæ, have gill pouches, usually placed at the caudal end, but all without any visible indication of a respiratory pigment."

As at present understood, respiration among Tracheates proceeds directly; atmospheric oxygen is led directly to the cells by the tracheae, while the blood acts primarily in the transportation of food and metabolic products. The question whether or not the blood may play a certain part in the transportation of gases is a point that merits investigation.

The following experiments on this subject were performed during spring, summer and fall of 1920, although some earlier observations are included in this paper.

II. Oxygen and Respiratory Proteins in Insect Blood.

To determine the oxygen content of insect blood directly is a matter of some difficulty, primarily because such reagents as are available are suitable only for considerable quantities of material, and are not adaptable for use with the microscopic quantities dealt with in the present experiments. For instance, an excellent reagent is pyrogallic acid, which in presence of an alkali absorbs oxygen with avidity. When testing for oxygen in the few drops of blood obtained from an insect, the difficulty lay in occluding atmospheric oxygen. Yet several experiments indicated the presence of oxygen in the blood; for the reagent darkened much more rapidly when applied to insect blood (pyrogallic acid turns brown to black with absorbed oxygen) than in the blank control tests. Yet at best this was unsatisfactory, as at least some portion of the reagent was in contact with atmospheric oxygen and tended to obscure the blood reaction. Nor could this be obviated with the use of cell slides and vaselined cover slips.

However, the same reagent was applied to Dytiscus larvæ by another method which was more effective. Freshly prepared pyrogallic acid solution was injected into the body cavity of the larvæ, followed by weak hydroxide. Death ensued quickly, in periods ranging from ten seconds to three minutes. Even before dissection the semi-transparent larvæ showed brown stains inside. The dissected larvæ showed brown blotches in the haemocoel and among the tissues, indicating that oxygen had been absorbed by the reagent. In the vicinity of the tracheæ the reagent was deeper brown, while the tracheæ themselves were almost black. Here, too, once the animal was cut open, atmospheric air had access to the reagent, which then blackened rapidly, obscured the tissues, and prevented more detailed study.

No doubt some of this reaction was due to oxygen dissolved in the blood serum, although the serum has no power to combine with oxygen like a respiratory protein. This oxygen, in mammalian serum, amounts to 94% of the amount soluble in water and the serum loses its supply with increased temperature.

These experiments, which were repeated a number of times with Dytiscus, Aeshna, Chironomus, and other larvæ, are significant from at least the qualitative standpoint. They do not indicate whether an active agent was present which combined loosely with the oxygen, or if the gas was in physical solution as in the water. The topic was, therefore broached from another angle—namely, that of the presence or absence of respiratory proteins. The obvious postulate was: If a respiratory pigment can be demonstrated in the blood of insects, its purpose must be to fix and transport oxygen. In that case, the blood of insects has the additional function of aiding in the respiration.

Such a respiratory protein need not necessarily be visible to the naked eye. For, in the first place, among the insects we are dealing with minute quantities of blood. Secondly, such a pigment would play only a subsidiary role, as the primary supply of oxygen is received by way of the tracheæ. The quantities of gas in solution in the blood

would, therefore, be minimal. Besides, even in such animals as crayfish, where the respiratory protein is known to be hemocyanin and bluish in color, when fully oxidized, the blood generally shows no color at all. It may be entirely transparent, or a pale to definite blue. Or it might be a pink to bright red, depending upon the amount of non-respiratory pigment (Tetronerythrin) present. In insects the blood, if colored at all, is bluish or greenish, forming black clots. There are exceptions to this, such as adult Dytiscus, in which the blood is saffron yellow to orange in color, although blue to purple in the larvæ. This color is not due to any respiratory protein, but to non-respiratory pigments, which are stored in the blood and elaborated into the external colors of the adult.

Assuming a respiratory pigment for the moment, there are two possibilities—the carrier in question may be either hemoglobin, or hemocyanin, or both, as in some mollusks. As far as known to the writer, hemocyanin has not been definitely reported for insects, while hemoglobin is known only for the Chironomid "blood-worms."

A considerable number of experiments were performed in the ensuing investigations. These experiments on respiratory proteins in insects have been described elsewhere, but since they bear on this discussion, a summary of the salient points will be necessary.

The problem as studied, presented the following phases: (1) Considering that conditions as met in aquatic insects postulate the presence of a respiratory protein, can such a protein be demonstrated? (2) If present, what is its nature? (3) Is it confined to aquatic insects possessing blood gills, or is it universal among insects?

For the first of these it was shown that the blood of insects reacts with the oxidation tests for hemoglobin (Guiac, O-tolidin, Benzidine), regardless of the species. Only Chironomid blood reacted with the hemin tests for hemoglobin. These tests showed that a respiratory protein was present.

In the second phase, considering the nature of this protein, two possibilities offered themselves. Of known proteins in Arthropoda there are only hemocyanin and hemoglobin. The first of these has a copper nucleus, the second is an iron compound. The hemin tests for hemoglobin showed that this protein is restricted to Chironomid "blood-worms" among the insects. It is a fact, however, that the blood of Aeshna, Anax, Dytiscus, and other insects showed isolated crystals resembling the hemin prisms. If present at all, therefore, hemoglobin is available only in infinitesimal quantities and may be disregarded.

For hemocyanin no direct tests are known. It was held, however, that if by some means copper could be shown to be present in insect blood in quantities as large as found in crayfish blood where the copper has a known function, then its role in both is identical. For this purpose a number of incinerations of insect and crayfish blood were made and the ashes tested for copper. Both reacted positively, showing copper in approximately equal amounts. It was therefore concluded that insects contain a respiratory of a nature similar to that of the crayfish, namely a hemocyanin.

In the third phases of that study, the distribution of copper in insects, the following list of animals were incinerated. (Numbers refer to number of separate incinerations, not to number of specimens):

Coleoptera: Dytiscus, 19; Gyrinus, 1; Harpalus, 1; Leptinotarsa, 1.
Hymenoptera: Apis, 2; Bombus, 1; Polistes, 2; Formica, 1.
Lepidoptera: Pieris, 4; Noctuidæ, 2.
Diptera: Musca, 4; Stomoxys, 2; Tachinid, 1; Stratiomyia, 1.
Hemiptera: Belostoma, 17; Ranatra, 1; Notonecta, 3; Gerris, 1; Corixa, 2; Aphis, 1, Leptocoris, 2.
Odonata: Anax and Aeshna, 4; Anax, 2; Aeshna, 15; Sympetrum, 4; Libellula, 4; Enallagma, 6.
Ephemeridæ: Several spp., 1.
Trichoptera: Several spp., 1.
Neuroptera: Myrmeleon, 3.
Megaloptera: Sialis, 1.
Isoptera: Termes, 1.
Orthoptera: Gryllus, 1; Ceuthophilus, 1; Locusta, 1; Melanoplus, 1; Dissosteira, 1.
Crustacea: Cambarus, 36; Hyalella, 2; Plankton, 1; Daphnia, 2; Microcystis, 1; Limnocalanus, 1.
Arachnida: Argiope, 1; Phaleana, 1; Spiders, 1.
Myriapoda: Centipeds, 1; millipeds, 1.
Annulata: Lumbricus, 1.
Mollusca: Snails, 5; slugs, 2.
Nemathelminthes: Ascaris, 1.
Protozoa: Volvox, 1.
Chordata: Snake blood, 1; human blood, 1; mouse, 1.

All of these, except human blood, reacted positively for copper, showing varying amounts.

As a final phase, the sources of copper were studied. Some 30 incinerations were made of twelve species of plants, all of which showed traces of copper. The soil and water were also tested, with positive results.

All of the Arthropoda studied showed a surprising uniformity in their reactions for copper. In practically all cases copper was present in quantities nearly equal to that of crayfish blood. This uniformity must have its significance. Copper in the quantities found could not come to the insects in their daily feeding, unless the tissues exercised a discriminating selection for the copper in their food. This copper must be functional, and because of the analogies pointed out it is interpreted as forming the nucleus of a respiratory protein, hemocyanin.

There is a further point to be considered. Unless we assume a blood protein to fix the oxygen, we cannot account for the presence of oxygen in the blood of insects living under practically anaerobic conditions, that is, insects living in warm and stagnant water.

Physically, oxygen tends to form a balance on both sides of a moist or immersed membrane. But since in the summer there are two factors which tend to decrease the oxygen supply available to insects in the water, namely organic decomposition and the heat of the water, the amount of oxygen, on a purely physical basis, would diminish also within the insect. Water contains its largest amount of dissolved oxygen at zero, and as the temperature rises this amount becomes less

and less, until it is zero at boiling point of the water. Furthermore, as the temperature of water rises above zero, decomposition and oxidation of wastes increase, so that the available supply of dissolved oxygen is used up in inverse ratio to its absorption by the water.

If respiration in aquatic insects, specifically in water-breathers, proceeded on the basis of a physical gas equilibrium on two sides of a membrane, the insect would soon show a deficiency of oxygen, and that at a time when it is most active and its metabolism demands a high rate of oxygenation. Yet this is precisely what we do ***not*** find. Regardless of the impoverished oxygen in warm pond or swamp water, the insect blood contains a plentiful supply of oxygen, and metabolism proceeds at its normal rate. Thus, in Aeshna, Dytiscus, and Chironomid larvæ, purposely kept in covered jars filled with decaying plant and animal matter, I found normal activity and the blood reacted copiously with injections of Pyrogallic acid. It is evident, therefore, that the blood possesses a protein which is capable of binding oxygen in excess of the amounts dissolved in the water. The incinerations showed that this protein is a copper compound.

From this standpoint, the various respiratory structures of insects, especially the gill filaments and gill pouches of Trichoptera larvæ and aquatic caterpillars, the caudal blood gills of Chironomus larvæ, of Culicid larvæ, Simulium larvæ, etc., acquire a real significance. These structures are purely blood gills, consisting of a thin cuticle and epidermis and their lumina are continuous with the haemocoel, so that the blood courses freely through them. With this type of gill, a respiratory protein to fix oxygen is very effective. On the other hand, unless such a protein is present, these structures loose their significance, in fact, appear useless as organs and inefficient physiologically.

III. Carbon Dioxide in Insect Blood.

The presence of carbon dioxide in insect blood has been reported frequently. During the summer of 1920 I was able to verify this fact in several series of experiments. The insects used were the same species utilized in the incinerations listed in the preceding section. The reagents employed were Potassium and Barium hydroxides, Lead acetate, Rosolic Acid, and halogen acids, the latter for carbonates. Of these Potassium hydroxide was perhaps the least satisfactory, as it is difficult to find the proper concentration of this reagent to give a definite reaction. Barium hydroxide reacts well with insect blood, yielding an amorphous precipitate. Lead acetate when applied directly will precipitate some of the blood proteins in addition to the carbon dioxide. When used with a micro-still, however, it is more effective and conclusive. I have used it as follows: A few drops of insect blood are caught on glass wool in a small glass or porcelain crucible, over which is placed a slide with a hanging drop of Lead acetate. Gentle heating releases the carbon dioxide, which forms Lead carbonate with the reagent.

As in the incinerations of insects for copper, crayfish blood was used as a control, with identical results. It seems then that in the latter the hemocyanin serves as a carrier for both oxygen and carbon dioxide, analogous to hemoglobin; and the presumption is that the same applies to insect blood.

Among other items, the Malpighian tubules of insects were studied as a possible exit for Carbon dioxide and carbonates. A number of experiments were made with the reagents mentioned on a variety of tubules, including those of bumblebees, larval and adult Dytiscus, Anax and Aeshna larvæ, Belostoma, Enallagma, and others. In summary, ten of eighty-one experiments showed positive results, the remaining seventy-one negative or doubtful. Even with a liberal allowance for error, these results are too insufficient to permit of any conclusions.

Elsewhere I have offered the suggestion (L. c., p. 93) that at least in aquatic larvæ the external chitin membrane may serve for the passage of carbon dioxide. This suggestion was based on some experiments on the permeability of the chitin membrane to gases, performed some years ago. However, this might apply to aquatic insects, it would not cover the conditions met in terrestrial stages.

IV. The Role of Insect Blood.

Hitherto our interpretation of the role of insect blood has been that the blood transports food, glandular products, waste, and pigments, and that it takes no part in the process of respiration. From the foregoing experiments it is evident that this interpretation must be amended to include respiration.

That the blood is active in transporting foods can be readily shown in testing fed and starved insects. After a meal the blood shows a large supply of nitrates, nitrites, and phosphates, the latter depending on the quality of food, whether rich or poor in phosphates. In a starved specimen, not fed for three or more days, none or only traces of these substances are indicated.

Glandular products include corpuscles, enzymes, some form of coagulin, and pigments. The pigments are carried passively in the blood stream, to be elaborated during the pupal period. The enzymes present are chiefly of the oxidative, histolytic, and autolytic types. Here also should be placed hemocyanin and hemoglobin, the respiratory proteins. In what tissues or organs these are elaborated has not been ascertained. Coagulin in some form must also be present, as the blood of insects clots readily on exposure to atmospheric air. This clot is generally black, but brown in adult Dytiscus. Whether this coagulin originates as a zymogen of the prothrombin type, forming thrombin, and combining with fibrinogen to form fibrin, as postulated for mammalian blood, is unknown.

Of gases the blood contains both oxygen and carbon dioxide, some probably dissolved in the blood serum, the major portion held by the hemocyanin present.

On this basis, the role of insect blood may be summarized as follows: The blood is instrumental (1) in circulating food, (2) transporting metabolic products (enzymes, pigments, etc.), (3) in respiration in the distribution of oxygen and removal of carbon dioxide.

Be it noted that the last of these, the role in respiration, is not confined to aquatic larvæ alone—that is, larvæ provided with blood gills. On the contrary, the role of the blood is identical in all insects, regardless of the stage. For the tests for respiratory proteins (oxidation and incineration) were performed on all types of insects, regardless of habitat, stage, and food habit of the species.

V. Summary.

1. Both oxygen and carbon dioxide are present in insect blood. A small portion of these gases is probably dissolved in the blood serum, the major portion is held by a respiratory protein.

2. A respiratory protein was demonstrated for all insects through reactions with oxidation tests for hemoglobin. Hemoglobin is possessed exclusively by Chironomid "blood-worms" among insects. All other insects show the presence of copper, which is interpreted as forming the nucleus of another respiratory pigment, hemocyanin.

3. This hemocyanin is possessed by all insects, regardless of stage, habitat, or food. The source of this copper was shown to be the water, soil, and food plants.

4. The role of insect blood is therefore, in addition to its recognized function of circulating food and metabolic products, to aid the tracheal system in the distribution of oxygen to the tissues and to remove the carbon dioxide.

VI. BIBLIOGRAPHY.

Muttkowski, R. A. The Respiration of Aquatic Insects: A Collective Review. Bull. Brooklyn Ent. Soc., 15, pp. 89-96, 131-140, 1920.

Rose, W. C., and **Bodansky, M.** Biochemical Studies on Marine Organisms: I. Copper in Marine Organisms. Jn. Biol. Chem., 44, pp. 99-112, 1920.

THE ENTOMOLOGICAL SOCIETY OF LONDON APPEALS FOR AID.

The fine old Entomological Society of London, founded in 1834, and which, since 1875, has been meeting at 11 Chandos Street by the courtesy of the Medical Society of London, has, through the growth of its library, outgrown its quarters and is practically forced to move. It has bought a house at 41 Queen's Gate, South Kensington, near the Natural History Museum, and is leasing a portion of the building to the Imperial Bureau of Entomology. The cost price of the property was ten thousand pounds, and an additional sum is required for furnishing.

The cost price has been largely met by subscriptions from members, both as donations and as loans, the loans being secured by a debenture on the property and bearing five per cent interest. After exhausting the available resources of the resident members, there still remains a sum approximating fifteen hundred pounds, and the Society is making an appeal to foreign members, to entomologists in the dominions, and to interested entomologists in other parts of the world. Donations and loans are received by the Treasurer of the Society, Mr. W. G. Sheldon, who may be addressed at 11 Chandos Street, Cavendish Square, London, W. I.

The London Society is the oldest of the great entomological societies, excepting the Entomological Society of France, which was founded a year earlier. Its Transactions and Proceedings have been largely used by American entomologists, and many of the latter when traveling abroad have been welcomed at the meetings of the Society and have cordially been given the use of the magnificent library.